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A BRYOCENOLOGICAL STUDY OF SOME EPIPHYTIC MOSSES OF A CENTRAL INDIANA WOODS

By BETTY L. WILSON

Mosses in general, and epiphytic species in particular, have received surprisingly little of the attention in America which they rightly deserve as an ecologically significant group. The ecological formations as distinguished in America (Weaver and Clements (21)) are closely affiliated with and largely defined by their respective climates. In other words, they may be said to be "macro-indicators" of climates.

Micro-climates are receiving considerable attention in Europe. These micro-climates refer to the local environmental conditions found in every situation, no matter how small. Such local conditions vary between ridges and ravines and other situations in which the differences are so small as not to be apparent, or expressed, in the dominant vegetation. Because of the greater sensitivity of mosses to environment, such micro-climates are sufficient to give expression to definite federations and associations in these plants. On the basis of such infinitely delicate adjustments to the environment, mosses, especially those which are epiphytic, may be considered "micro-indicators."

Ochsner (15) has said, "The vegetation of a country is the visible expression of its climate," and, according to him, the moss types may indicate moisture (dew, rain, humidity), temperature and light relationships, besides other more local conditions. Concerning one of his associations he says, "Probably one could designate them as rain indicators, since the abundance of their presence is about comparable to the amount of rainfall." If mosses are to be utilized as indicators of local climate within a dominant association, studies must be made throughout the country to provide, if possible, a basic standard for a universal system. The present study of moss societies revealed some interesting facts as to the relationship of epiphytic mosses to the host tree, the physiographic location and the immediate micro-climate.

REVIEW OF LITERATURE

American work in bryocenology has hardly been of a truly ecological nature, since standard ecological methods have not been used. Species have been listed and successions named with no data other than those

gained from extensive instead of intensive methods. European work, on the other hand, has been more intensive and systematic in its presentation. Systems of classification have been proposed, and technique of ecological caliber marks the methods.

Cooper (5), in his study of the ecological succession of mosses on Isle Royale, approaches the European system in his presentation. He does not mention, however, how the data for his diagrams were obtained. Miss Taylor's work (19) is voluminous, but lacks the diagnostic comparisons possible only through tables and figures based on data obtained by standard methods of sampling. These are essential to a concrete picture of the vegetation. She presents two tables on mosses, in which the presence of species is shown in associations of xerarch and hydrarch successions. In the flood plain which was studied, she found practically no mosses, which she attributed to the deposition of silt. The findings described in the present paper indicate that silt deposits do not prevent growth of mosses. The same criticism of a lack of statistical ecological methods likewise applies to the presentation of succession by Glenn and Welch (8). The work of Montgomery (14) and Robinove and LaRue (18) concerned itself chiefly with the soil reactions which certain mosses could endure. On the whole, such bryocenological data as we have in America have been gathered without application of statistical ecological methods.

Gams (6) has formulated the most complete and workable system of ecological classification for mosses. His system and methods of study have been followed in the present investigation, which is confined to the epixylia of the epiphytia of his classification.

LOCATION AND CHARACTERISTICS OF REGION STUDIED

The woods studied for its epiphytic mosses is in the Fort Benjamin Harrison Military Reservation, which is nine miles northeast of Indianapolis. The woods under consideration shows no evidence of any cultural disturbance in the last fifty years, with the exception of the flood plain region which adjoins an old field now in stages of secondary succession. The area is removed from the activities of the military forces. The woods has a rolling topography consisting of upland and ravines, dissected by streams. The tops of the ridges are plateau-like with no sharp ridges, so that there is not sufficient topographic control to cause

a marked change in the climax forest. The major stream flowing through the area is Fall creek, into which the smaller streams flow. These smaller streams are dry, or nearly so, during the summer. The soil is of glacial origin, with considerable boulders and gravel and without exposed bedrock.

Outside of the flood plain proper, the forest is a typical dense *Fagus-Acer* climax, with some representation of *Quercus alba* on the drier slopes. *Ulmus americana* and *U. fulva* are distributed throughout the forest. Some of the beech and maple range up to thirty inches in diameter. There is considerable leaf litter on the forest floor, which is nearly free of all vegetation except for a spring flora. The flood plain is dominated by species of *Acer*, *Platanus*, *Fraxinus*, *Ulmus* and *Populus*. This area was overflowed in 1933 by the waters of Fall creek, which left an accumulation of silt.

Humidity is of particular importance to the epiphytes. The humidity record for Indianapolis over a three-year period shows for 1932 an average variation from 46 per cent at noon to 79 per cent in the morning; for 1933, from 40 per cent at noon to 79 per cent in the morning; and for 1934, from 34 per cent at noon to 84 per cent in the morning. The low humidity records were from May, June, July and August, and the high largely from August and September.

The direction of the prevailing winds is taken above Indianapolis every minute by the Weather Bureau (20). Their monthly averages for 1934 are as follows: January-April, south; May-June, southwest; July-November, south; December, west.

METHODS

A study of the epiphytic mosses involves certain taxonomic difficulties which must be given special consideration here. In collecting, many species may escape the eye unless the area studied is examined very closely. Even then there are species present which can be identified only with the aid of a microscope. For this reason it is necessary to make many more collections than seems to be warranted by the appearance to the eye or even under a hand lens. A typical example of two species presenting such difficulty are *Homomallium adnatum* and *Platygyrium repens*. Their outward appearance is often identical, but to make matters more confusing, vegetative specimens are often difficult to distinguish under a microscope. *P. repens* has median cells 8:1 and

a more slender acumination, while *H. adnatum* has median cells 4-7:1 and a less acuminate leaf apex, but gradations may be found from one extreme to the other. (Grout (10) says they probably hybridize.) *Platygyrium* may be distinguished by the gemmæ if they are found, but they are not always present.

Epiphytic mosses are seldom found fruiting, which introduces another difficulty for identification. In the two hundred specimens collected for this paper, however, there was but one (an acrocarpous form) which could not be identified because of lack of fruit. This was present on one tree only and in no significant abundance.

North was located on the tree by aid of a compass and marked with a thumb tack. The circumference of the trunk was determined at a meter and a half from the ground, which was the upper limit used in this study. The area was then divided into four equal parts constituting the north, west, south and east sides of the tree. Halfway between each cardinal point of the compass, strings were suspended, delimiting the north, west, south and east sides. At five dm. from the ground, or the so-called "base" of the tree, another measurement was made. Where trees had a conspicuous root spread, this was also measured.

The tree trunk was then drawn to scale upon graph paper as though it had been split and flattened out on one plane, with the split occurring in the middle of the south side. Each small square in the diagram represents 4.0 cm. on a side. The system of presentation given by Gams (6) has been followed. A detailed description is given under "Observations."

In order to measure moss colonies accurately, a wire frame 2.0 dm. square was marked off into squares 4.0 cm. on a side. This area was equivalent to that represented by each square of the graph and facilitated charting. Beginning with the north side, the mosses were sketched in as they appeared on the tree trunk (Figures 4-14).

The investigation was limited to the epiphytes on *Fagus grandifolia*, *Acer saccharum* and *Ulmus americana*: five trees of each from the ravine in the vicinity of the stream, and five of each on the ridge top were studied. Five additional trees of *Ulmus* were also studied in the adjoining lowland. Little attention was paid to the liverworts and lichens, other than to sketch them in when their presence was conspicuous.

Collections were made from every patch of moss for microscopic determination. In all, two hundred collections were made and identified

by the aid of Grout's "Mosses with Hand Lens and Microscope" and such issues of his "Moss Flora of North America" as have been published to date. Nomenclature is that used in his Moss Flora, or, for species not yet treated in those volumes, that of "Mosses with Hand Lens and Microscope." The charting of trees and collecting was done in March and April of 1935.

Doubtful species were either checked or identified by G. B. Kaiser and L. E. Anderson, of the Sullivant Moss Society.

OBSERVATIONS

The following is a list of the species found in the study. The synonyms given in parenthesis are species names in Grout's "Mosses with Hand Lens and Microscope," which he has changed in his "Moss Flora of North America."

1. *Homomallium adnatum*
(*Amblystegiella adnata*)
2. *Platygyrium repens*
3. *Anomodon attenuatus*
4. *A. minor*
5. *A. tristis*
6. *A. rostratus*
7. *Schwetschkeopsis denticulata*
(*Leskea denticulata*)
8. *Amblystegium varium*
9. *Leskea gracilescens*
10. *Entodon seductrix*
11. *E. cladorrhizans*
12. *Thuidium minutulum*
13. *Orthotrichum Schimperii*
(*O. pumilum*)
14. *Plagiothecium micans*
15. *Leskea arenicola*
16. *Mnium cuspidatum*
17. *Eurhynchium serrulatum*
18. *Brachythecium velutinum*
19. *Leucodon julaceous*
20. *Homalotheciella subcapillata*
21. Unidentified species

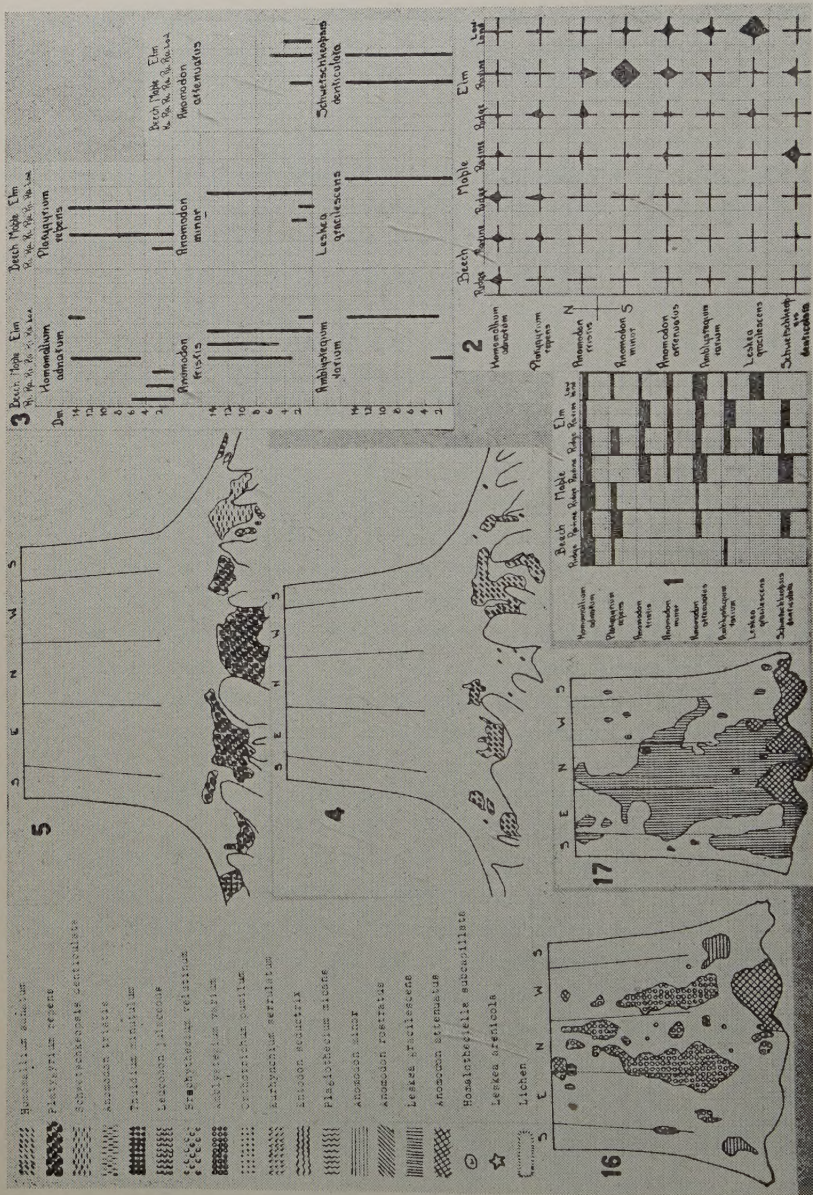


Fig. 1. Showing presence of eight most prevalent mosses. Each small space represents one tree.

Fig. 2. Coverage classes of eight most prevalent species. Each small space represents one coverage class.

Fig. 3. Altitudinal distribution of eight most prevalent species. Only patches one decimeter square or more considered.

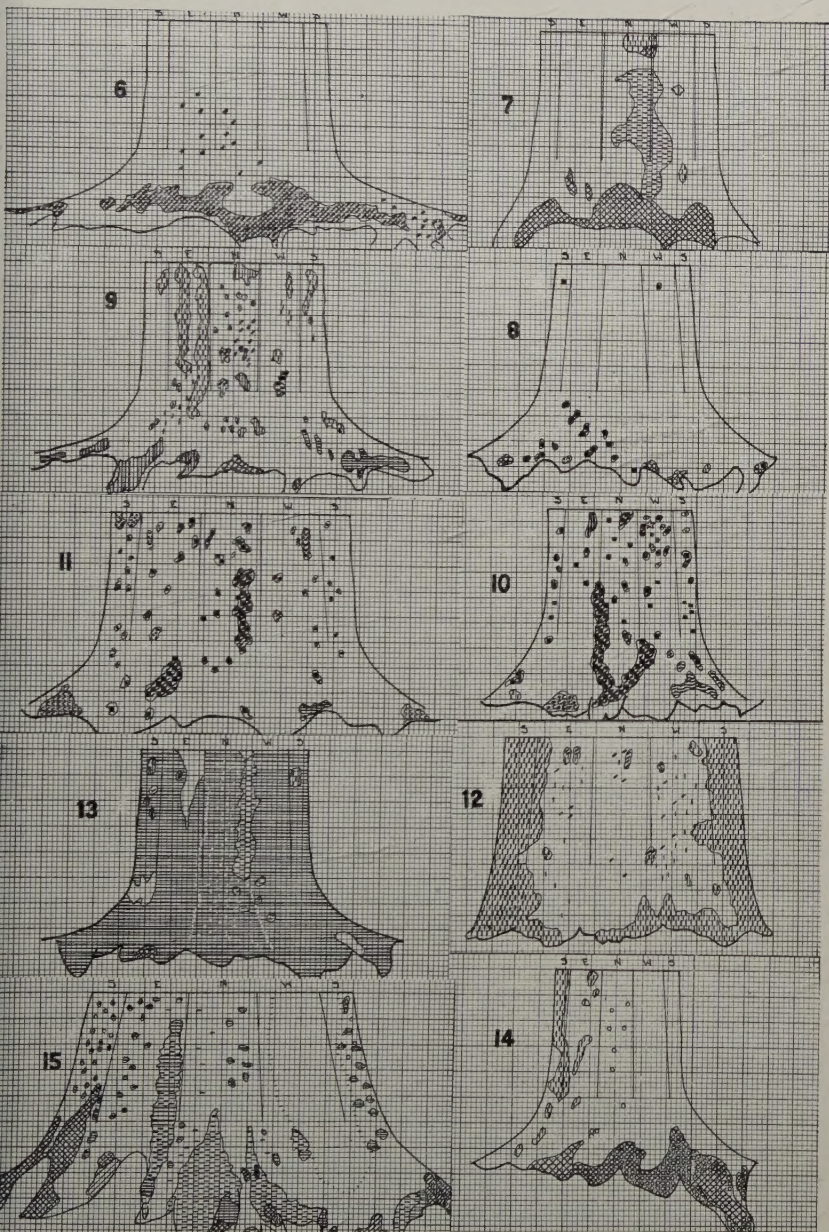


Fig. 6. Typical *Acer saccharum* as found on ridge.
 Fig. 7. Typical *Acer saccharum* as found in ravine.
 Figs. 8-11. Examples of *Ulmus americana* as found on ridge.
 Figs. 12-15. Examples of *Ulmus americana* as found in ravine.
 Fig. 16. Exception to the typical *Ulmus americana* as found in the lowland.
 Fig. 17. Typical *Ulmus americana* as found in the lowland.

From the distribution of mosses on the trees studied, it is apparent that different species of epiphytic mosses dominate under different physiographic conditions which are not extreme enough to be apparent in the higher vegetation. Within each different physiographic unit, however, there are smaller units of epiphytic vegetation controlled by the nature of species of the host tree and minute climatic differences. These units so defined by moisture are expressed in the various associations.

In the presentation of these various associations, the system suggested by Gams (6) has been followed. The federation, of which there is but one in this paper, is designated by the ending -ion, covering the several floristically related types of the same region. The sociotypes are marked by the termination -etum and signify the type societies abstracted from similar concrete societies. Federations are named from the most representative genus (or species), and sociotypes by the dominant species.

FEDERATION: *Homomallion adnatum*

Homomallium adnatum controls the federation for both ridge and ravine. It has the following frequencies: ridge *Fagus*, 100; ridge *Acer*, 100; ravine *Fagus*, 60; ridge *Ulmus*, 60; ravine *Acer*, 60; and ravine *Ulmus*, 20. From this it may be seen that *Homomallium adnatum* has a frequency on all specimens of *Fagus* studied of 80 per cent, on *Acer* 80 per cent, and on *Ulmus* 40 per cent. (See Table II.) Frequency of this species based on physiographic features shows for the ridge top 87 per cent, and for the ravine 47 per cent. The total frequency, then, amounts to 67 per cent, making it the most representative species.

ASSOCIATION: *Homomallietum adnatum*

The association dominates both *Fagus* and *Acer* on ridges (Figures 4 and 6), there being scarcely any difference in the appearance of the moss flora on these trees. On ridge *Acer*, under protection of climbing vines and bulges in the trunk, moss is able to grow above the base, to which it is restricted on *Fagus* because of the smooth character of the bark. The moss stems were tightly appressed to the bark, but with the ends of the branches often more or less erect. The association is characterized by the small number of species growing in it. There were but two other species besides the dominant: *Platygyrium repens* and

Amblystegium varium. The latter occurred but once and that in a mixed colony. Both of these, like the dominant species, are appressed mosses.

In investigating the moisture absorbing quality of bark (Table I), it was found that bark of *Fagus* absorbed less water from a saturated atmosphere than did that of *Acer*, while bark of *Ulmus* absorbed the most. The results found in this study indicate that the moisture-absorbing ability of the bark is of direct benefit to the epiphytic mosses. Assuming bark of *Fagus* to present the most xerophytic conditions of any species studied, and the ridge top to exceed the other physiographic locations in xerophytism, *Homomallietum* may be considered as the association requiring the least moisture of any observed. *Homomallium adnatum*, while apparently able to ecise under conditions of less moisture than other species present in the region, nevertheless shows a preference for the north side of the ridge trees.

TABLE I

MOISTURE ABSORBED FROM A SATURATED ATMOSPHERE BY THE
BARK OF CERTAIN TREES

TREE	Water Absorbed (Gms.)	Per Cent Water Absorbed	Average
<i>Ulmus americana</i> 1.....	1.1020	21.2	
<i>Ulmus americana</i> 2.....	.7668	18.9	20.2
<i>Ulmus americana</i> 3.....	1.2455	20.6	
<i>Acer saccharum</i> 1.....	1.4754	16.4	
<i>Acer saccharum</i> 2.....	1.8299	18.8	17.6
<i>Acer saccharum</i> 3.....	1.2873	17.7	
<i>Fagus grandifolia</i> 1.....	1.3411	13.4	
<i>Fagus grandifolia</i> 2.....	.889	13.5	13.5
<i>Fagus grandifolia</i> 3.....	1.1832	13.7	

ASSOCIATION: *Platygyrietum repens*

Platygyrium repens, often difficult to distinguish from *Homomallium adnatum*, approximated more closely the habitat requirements of the latter than any other species found. The bark moisture data and physiographic location showed that the *Platygyrietum repens* ranks next to *Homomallietum* in moisture requirements. *Platygyrietum repens* controlled on *Fagus* in the ravine and on *Ulmus* on the ridge when they are near the woods margins (Figures 5, 8, 10 and 11). *Ulmus* on the

ridge farther in the woods supported *Anomodetum*, the association next considered.

With an increase in moisture conditions comes an increase in the number of species. In the *Platygyrietum repens* on *Ulmus* on the ridge near the field, twelve species were present in an open association, viz., *Platygyrium repens*, *Amblystegium varium*, *Eurhynchium serrulatum*, *Leskea gracilescens*, *L. arenicola*, *Brachythecium velutinum*, *Orthotrichum pumilum*, *Entodon seductrix*, *Homomallium adnatum*, *Mnium cuspidatum*, *Leucodon julaceus*, *Anomodon minor*.

In the *Platygyrietum* on *Fagus* in the ravine there were but six species limited to the base of the trees, viz., *Homomallium adnatum*, *Schwetschkeopsis denticulata*, *Anomodon attenuatus*, *Thuidium minutulum*, and an unidentified species in addition to *P. repens*. All of these, except *Platygyrium* and *Homomallium*, occurred but sparingly. The presence of twelve species on *Ulmus* on the ridge and only six on *Fagus* in the ravine may be significant in light of the greater moisture-absorbing capacity of bark of *Ulmus*.

Orthotrichum pumilum was the only obligative epiphyte found in this study. It was confined to the *Platygyrietum* on *Ulmus* on the ridge near the field, and it showed a very peculiar distribution. It was not seen in any other location except in the flood plain where it occurred on the tree too high to be considered. It was observed to avoid the north side as well as the bases of the trees on which it was growing, preferring the upper limits of the areas studied. It grew typically in small patches and was chiefly confined to the bark fissures. It occurred only on *Ulmus* near the margin of the woods. Ochsner (15) concluded that this species was dependent on the rainfall.

The open association of the *Platygyrietum* on the ridge and the presence of the several other species indicate that a very slight change in the micro-climate might easily swing the dominance to another species. This is emphasized by the change of the dominance to another species on *Ulmus* farther from the field, as seen in the next association.

ASSOCIATION: *Anomodetum tristis*

This association closely resembles the *Platygyrietum* of the ridge in several ways. It occurs on *Ulmus* on the ridge, although at a greater distance from the field. It is an open association and is characterized by the presence of several species (Figure 9).

The species growing in this association, although large in number, are small in coverage, viz., *Anomodon tristis*, *Schwetschkeopsis denticulata*, *Leskea gracilescens*, *A. minor*, *Homomallium adnatum*, *Plagiothecium micans*, *A. attenuatus*. The number of species here is not so large as in the *Platygyrietum* on *Ulmus* on the ridge. *A. tristis* occurs again on *Ulmus* in the ravine, nearly covering one tree, as does *A. minor*. *Leskea gracilescens* controls the association on *Ulmus* in the flood plain.

ASSOCIATION: *Anomodetum*

Because of the more favorable habitat of *Ulmus* in the ravine, the minute micro-climatic variations allow for a more conspicuous expression in the moss flora. Unfortunately, however, these expressions were also controlled, or apparently so, by the contour of the tree in so many cases as to leave the determination of the dominance questionable (Figures 14 and 15). For this reason those trees which showed a complete dominance were taken as standard; and, since one of these was covered by *Anomodon minor* and one by *A. tristis*, the association must be denoted as *Anomodetum* (Figures 12 and 13). Of those trees in which the contour seemed to control the dominance, one, because of deep furrows, allowed *Schwetschkeopsis* to cover sufficient space to be considered dominant (Figure 15). One tree leaning to the south allowed *A. attenuatus* to dominate; and another, with narrow trunk but wide root spread and available space for dust to collect, showed *Amblystegium varium* to predominate slightly (Figure 14).

This association, besides its peculiarity of dominance, is distinguished from all the preceding by its amount of coverage. Considering the so-called "standard" trees, the association is a closed one. The tree controlled by *Anomodon minor* is completely covered but for a negligible space occupied by *Schwetschkeopsis*. *A. tristis* likewise showed a conspicuous coverage. The association showed all of the *Anomodons* found in any other association and one that was found nowhere else, viz., *A. minor*, *A. tristis*, *A. attenuatus* and *A. rostratus*. The last was found on but one tree and in no great abundance. *Schwetschkeopsis denticulata* and *Amblystegium varium* were conspicuous. Other species occurring but sparingly were *Homalotheciella subcapillata*, *Leskea gracilescens* and *Homomallium adnatum*. The trees of this association were protected by the ravine from desiccating winds, and they were in the vicinity of a small stream, sometimes dry, but where moist conditions prevail.

The Anomodons may be said to be generally moisture-loving mosses, capable of crowding out other species when the moisture is sufficient for their growth. It may be noted that these Anomodons have much of their surface free from the bark. *A. tristis* in particular is a very loosely attached form with but few branches. Its leaves when dry are tightly appressed to the stem. *A. attenuatus* is a heavy mat-forming species, densely branched. It has two kinds of branches, viz., very slender, flagelliform branches with small leaves, and larger stem-like branches. These latter when dry have the young tips curled under, presenting the blunt, hunched surface of the erect branches to the weather. Garjeanne (7) says that new shoots are much less resistant than the older parts. The stem leaves are not much changed when dry.

Anomodon minor, as it grew here, approached *A. tristis* in general appearance. It was but loosely attached and sparingly branched. These Anomodons react immediately to water. When a drop of rain falls on a branch, the papillose leaves expand with incredible swiftness. The Anomodons typically formed closed associations, with the exception of *A. tristis*. This species is often found mixed with species of a different form (*Homomallium*) because of its less dense habit.

ASSOCIATION: *Schwetschkeopsetum denticulata*

Although this association occupied apparently the same physiographic location as the Anomodetum, it presented exactly the opposite characteristics. While the Anomodetum on *Ulmus* in the ravine showed a different aspect on every tree, *Schwetschkeopsetum* is a clearly defined association on *Acer* in the ravine, and every tree displayed a remarkably similar moss flora (Figure 7). The association was practically a closed one and limited to the north side of the trees. It typically showed an altitudinal zonation, beginning with *Anomodon attenuatus* at the base, and *Schwetschkeopsis* occupying most of the remainder of the north side. *A. tristis* was in varied amounts and places. It occurred usually in small patches and seemed to be crowded out by *Schwetschkeopsis*, as the latter was by *A. attenuatus* on the tree bases. *A. tristis* showed a frequency here of 80 per cent (Table II). It sometimes grew associated with *Homomallium adnatum* on the north, but found its maximum growth on the east and west sides. *Homomallium* here is limited to higher parts of the trees than was the case on the ridge.

The only species that seemed to show a preference for the south side

was *A. minor*, and it was found on but one tree. *Entodon seductrix* was in two very small patches. On one of the trees a sprout grew from the base of the south side. From the protection afforded by this, Schwetschkeopsis was able to grow on the south side. Whether it was the light condition that was so affected by the sapling, or the moisture, is uncertain. Very likely the two are so closely associated in their influence on this species that one cannot be isolated from the other. Schwetschkeopsis makes a silky looking mat on the tree and forms a closed association.

Because of the typical similarity of the epiphytes on each tree, this sociotype is probably less sensitive to the habitat conditions than the Anomodetum on *Ulmus* in the ravine.

ASSOCIATION: *Leskeetum gracilescens*

Since *Fagus* and *Acer saccharum* are absent in the lowland, *Ulmus* was the only tree species studied for its moss flora. *Leskea gracilescens* is as clearly the dominant here as Schwetschkeopsis is on *Acer* in the ravine (Figure 17). The water of Fall creek repeatedly rises over this flood plain area and leaves a fine deposit of silt on the trees. The dominant trees are *Platanus* and *Ulmus*. *Leskea* completely controlled on all the trees studied but one, on which *Amblystegium varium* was found to dominate (Figure 16). *Leskea* shows a strong preference for the north side, although on one tree it spread until it covered all but the west and southwest sides. The silt deposit or dust is the probable limiting factor for *L. gracilescens*. Grout (10) says that this species may also be found growing on decaying logs and soil. Epiphytic species often are facultative epiphytes, frequently growing on stones, but a few epiphytic species are known to grow on soil also.

Anomodon attenuatus occupies much the same place here as in the Schwetschkeopsetum, except that it is not confined to any one side but was found on all sides at the bases of *Ulmus*. *Amblystegium varium* assumed dominant proportions on one tree. Other species found growing in small colonies in the association were: *Entodon seductrix*, *E. cladorrhizans* (only a few stems), *Homomallium adnatum*, *Orthotrichum Schimperi*, *Anomodon minor* and *A. tristis*.

TABLE II
SOME FREQUENCY INDEX COMPARISONS BY PER CENT

	RIDGE			RAVINE				Ulmus	Ridge	Ravine	Frequency
	F	A	U	F	A	U	Fagus				
<i>Anomodon attenuatus</i>	0	20	40	40	100	60	20	60	20	67	43
<i>Homomallum adnatum</i>	100	100	60	60	60	20	80	80	87	47	67
<i>Anomodon tristis</i>	0	0	40	0	80	80	0	40	13	53	33
<i>Anomodon minor</i>	0	0	40	0	20	60	0	10	13	27	20
<i>Leskea gracilescens</i>	0	0	80	0	0	0	0	0	27	0	13
<i>Amblystegium varium</i>	20	0	40	0	0	80	10	0	20	27	23
<i>Schwetschkeopsis denticulata</i>	0	0	20	60	100	60	30	50	7	73	40
<i>Platygyrium repens</i>	20	40	60	80	0	0	50	20	40	27	33

HYDROGEN-ION REACTIONS OF BARK

Nine samples of bark were taken from two trees of *Acer*, eight samples from two trees of *Ulmus* and eight from two trees of *Fagus*, all growing on the ridge. The bark was cut into thin shavings and tested for acidity by the Youden quinhydrone method. The results showed the pH to range as follows: *Acer saccharum*, 5.5-6.93, average, 5.72; *Ulmus*, 5.63-6.53, average, 5.94; and *Fagus*, 4.72-5.38, average, 4.96. Bark, thus, showed a decided acid reaction.

BARK MOISTURE

The fact that different species of trees growing under approximately the same physiographic conditions often supported different moss associations suggested that bark moisture conditions might play a dominant role. In order to test out this hypothesis, an experiment was conducted in the following manner: Bark was collected from three trees each of *Fagus*, *Acer* and *Ulmus*. It was brought into the laboratory in soil cans and thoroughly dried at a temperature of 100 degrees C. for four days. The bark was then taken from the ovens and weighed in the cans. A low dish of warm water was placed on a tray with the cans of bark in a circle around it. The whole was covered with a bell jar and allowed to remain for a week. At the end of this time the atmosphere within was doubtless saturated. Removing each can separately, the bark was again weighed and the results tabulated (Table I). The percentage of moisture was based on the dry weight of the bark.

The average water absorbed by *Fagus* was 13.5 per cent, by *Acer* 17.6 per cent, and by *Ulmus* 20.4 per cent. These figures offer an explanation for the differences between the epiphytic moss flora of *Acer* and *Ulmus* in the ravine and *Acer* and *Ulmus* on the ridge.

DISCUSSION

A study of the distribution of moss species on the trees reveals a very pronounced selectivity. It is this sensitive selective power of mosses which stamps them as micro-indicators. At present, the methods for measuring light and moisture conditions of the atmosphere immediately next to the bark, or in the fissures, are inadequate.

It is impossible under the conditions of this study to isolate any one

factor as being the limiting factor. There can be no harm, however, in pointing out noticeable environmental factors if there is an understanding of the inseparable nature of the whole of the life factors. This inseparability was indicated by Ochsner when he said, "The greater the amount of light the greater will usually also be the danger of desiccation." Once the limiting factors for these species can be determined, their value as micro-indicators will begin.

BARK MOISTURE

The distribution of species is not controlled entirely by physiographic conditions. From a comparison of the associations of either the ridge or the ravine, it is evident that some other factor is of importance equal to the physiographic location. The distribution of the mosses suggests that this factor may be difference in bark moisture, and falls in line with the experiment previously described (Table I), which showed that small quantities of bark from *Acer saccharum* absorbed 4.1 per cent more water from a saturated atmosphere than that of *Fagus*; and *Ulmus* absorbed 2.8 per cent more than that of *Acer*.

Certain aspects relating to the moisture of bark are indicated by the mosses themselves. These are summarized here: The number of moss species growing in a given habitat is more or less indicative of the environment, the same as in higher vegetation. Optimum habitats tend to show a smaller number of species than rigorous habitats, if the latter are not too extreme in their conditions. Optimum habitats allow one species to dominate and "close" the association, while more rigorous habitats are not sufficiently favorable for any one species to become a dominant. On the ridge, *Acer* and *Fagus* each supported two species, while *Ulmus* supported 15; in the ravine *Fagus* and *Acer* each supported five species, while *Ulmus* supported nine. Apparently *Fagus* and *Acer* on the ridge excluded most species by their more rigorous habitats, while *Fagus*, *Acer* and *Ulmus* in the ravine and *Ulmus* on the ridge were more favorable moss habitats.

In the ravine, where conditions more nearly reach the optimum, each species of tree studied supported a different moss association. For *Fagus* it was *Platygyrietum*; for *Acer*, *Schwetschkeopsetum*, and for *Ulmus*, *Anomodetum*. Of the eight species selected as most representative from the standpoint of frequency and coverage, four occurred entirely, or almost so, on *Ulmus*. These four species are *Anomodon*

minor, *A. tristis*, *Leskea gracilescens* and *Amblystegium varium*. The presence of *Leskea gracilescens* on *Ulmus* only may be more or less accidental, as its distribution seems to have been controlled largely by dust and silt, and *Ulmus* was the only species studied which presented such a substratum to any extent. However, the presence of *Anomodon minor* and *Amblystegium varium* on *Ulmus*, to the exclusion of nearly every other tree studied, is particularly noticeable.

Harvey (11) says that "differences as great as 25 degrees C. may exist between the temperatures of the south and north sides of (internal) tree trunks." He also says that "The air temperature shows some fluctuation with sun and shade, but to no such marked degree as the bark." Whether this temperature variation has any effect on epiphytes is uncertain, but it may play a part in the bark moisture of the host trees.

OTHER FACTORS

Anomodon tristis, by its tendency to shun the north side of trees, may be assumed to be affected about as much by light conditions as by moisture. At no time did it show any particular development on the north side. On the ridge its maximum coverage was on the east, in the ravine the south, and in the lowland the greatest coverage was on the southwest side. Assuming that for *Ulmus* in the ravine the ridges cut off the influence of the wind, that moisture was plentiful on all sides of the tree, the only explanation left for the complete southern coverage is the light factor. If its coverage on the south were because of an affinity for less moisture it would not be likely to grow to the base as it did (Figure 12). The same theory seems to hold true for *A. minor*, but with moisture more important, and light less, than in *A. tristis*.

Homomallium adnatum, *Schwetschkeopsis denticulata* and *Anomodon attenuatus* are probably controlled largely by moisture conditions. Of these, *Homomallium* seemed to prefer the drier situations, as expressed by its dominance on the ridge and its tendency, when present in the ravine, to be limited to the higher parts of the zones studied. *Schwetschkeopsis denticulata* showed a preference for medium-moist, shady substrata by its abundance on the north side of trees in the ravine. Abundance was reduced, however, on *Ulmus* as compared with *Acer*. It is possible that the greater moisture content of *Ulmus* bark produced a less favorable habitat. Only very moist conditions seemed adequate

for *Anomodon attenuatus*, as expressed by its restriction to the bases of trees even in moist localities. Miss Taylor (19) claims that "*Anomodon attenuatus* occurs in dry situations, usually on tree bases," and by dry we may assume that she means comparatively so, as against the moisture contained in soils.

The presence of noticeable quantities of silt deposit on the north side of trees of the flood plain cannot escape attention, when trying to account for the dominance of *Leskea gracilescens*. Apparently dust or silt is the limiting factor. This hypothesis gains more weight when it is recalled that *Leskea gracilescens* is one of very few epiphytes, according to Grout (10), which also grows on soil. *Amblystegium varium* is another, and likewise seems to be limited to dust deposits. Richards (17) points out that epiphytic mosses vary in species, depending on chemical nature of soil deposits on tree bark. In unprotected places, wind may be a major factor in affecting the growth of epiphytes. Ochsner (15) has shown that "moss vegetation is especially luxuriantly developed in valleys and depressions which are not subjected to desiccating winds," and this seems to hold for the ravine in this study. Richards (17) attributes the greater coverage of the southwest side of trees in England to the wind. "Its effects are particularly obvious on epiphytes. In England trees are usually moss-covered only on the western and southwestern sides (which face the prevailing wind). This effect is probably due to the rain being driven against the tree trunks." Results of the present study are not in agreement with Richards' observations.

HYDROGEN-ION REACTIONS OF BARK

Certain species of mosses for some time have been considered as indicators of acidity. In spite of the fact that much work has been done, it is not possible at present to arrive at definite conclusions. Richards (17) has shown that there is a definite range of pH, together with an optimum point, for each moss species. European workers have found that there is a range which is closely associated with other environmental variations. For instance, a moss which has been found to be calcicole in one habitat may be calcifuge in another under different conditions.

Amann (1) and Richards (17) both seem to favor the conclusion that each species has a definite pH preference. They remark, however,

on the possibility of making false deductions. For example, a calcifuge species may be growing on limestone if there has been considerable leaching or if there is a thin layer of humus. Robinove and LaRue (18) have found that moss species have a much wider range of pH than formerly supposed.

Montgomery (14) maintains that "most acid-loving mosses are acrocarps, most alkaline mosses are pleurocarps." He also found that epiphytic mosses gave a neutral to alkaline reaction, which he mentions as typical for the group. In the present study the bark of some trees gave a pH average of 4.96 to 5.94.

DISTRIBUTIONAL FACTORS

FIDELITY

The fidelity of certain species is essential to the classification of mosses as micro-indicators. Clements (3) holds that the dominant is the most important of all indicators. Ochsner (15) maintains that we would destroy the floristic-ecologic unit of species combination if we were to consider the ever-present species as alone diagnostic of the association. In fact, these constant species give less information about the association life condition than his so-called "character-species" which show a much smaller ecologic amplitude than the former, and are much better suited to represent the association, even though they are not constant and usually are not ever-present. Ochsner's theory would thus emphasize the fidelity of association species rather than constancy.

Lippmaa (13) apparently does not consider fidelity as sufficiently distinct to be significant. He maintains that chance plays too important a role in the distribution of species. Ochsner (15) maintains that "in epiphytic associations the degree of association fidelity is closely related to the degree of fidelity to the habitat."

FREQUENCY

As in other data given for mosses, frequency is best studied along with the coverage figures (Figure 2). The difficulty involved with the interpretation of frequency figures arises from the impossibility of considering individual moss plants. The individual is necessarily abandoned for a consideration of the coverage. Coverage for any species

on any one tree may range from 1 sq. cm. to total coverage; in frequency data, one would receive the same attention as the other, thereby tending to place all coverage classes on an equal. In a general way, however, frequency figures may be valuable, as they are in determining the federation. The federation in this study received its character name by reason of the high frequency for *Homomallium adnatum* (67 per cent) as compared to the next highest total frequency (43 per cent) for *Anomodon attenuatus*. An idea of the frequency of the most representative species is best obtained from Table II. Frequency figures for the lowland were not included, since *Ulmus* was the only substrate studied.

Homomallium adnatum, already designated as preferring drier habitats than the other species, has its greatest coverage on the north side of the ridge *Acer*, but on the south side of the ravine *Acer*, while it was practically absent from the ravine *Ulmus*. The data on bark moisture for these species of trees make these distributions more significant. The smooth character of the bark of *Fagus* on all but the very base accounts for the lack of mosses there.

In the ravine a few trees were observed which were leaning slightly. In all such cases, moss could be seen growing to the top of the tree on the upper side.

Altitudinal distribution of species, expressed in graphic form, does not always give a true picture of the situation. On trees which have bulges, moss may be found in considerable abundance above such a protrusion where the rain is retained for a time. Such colonies may again occur where lianas are growing against the tree. Recording these colonies on the figures leads to a wrong impression unless the data are studied in connection with the tree diagrams themselves.

SOCIOTYPES

The sociotypes were distinct. They were defined by a three-fold control: host tree, physiographic location and micro-climate. The one factor, however, common to these three habitat elements, and which was, therefore, the ultimate limiting control, was moisture.

The ridge presents three sociotypes: on *Fagus* and *Acer*, *Homomallietum adnatum*; on *Ulmus* near an old field, *Platygyrietum repens*; and on elm farther in the woods, *Anomodetum tristis*. The ravine also shows three sociotypes: on *Fagus*, *Platygyrietum repens*; on *Acer*,

Schwetschkeopsetum denticulata, and on *Ulmus*, the *Anomodetums*. *Ulmus* of the flood plain is dominated by the *Leskeetum gracilescens*.

A tentative arrangement of the associations on the basis of moisture requirement, and beginning with the least, would be: *Homomallietum adnatum*, *Platygyrietum repens*, *Anomodetum tristis*, *Schwetschkeopsetum denticulata* and *Anomodetum* (*minor* and *attenuatus*).

SUMMARY

1. This paper attempts to present a conception of the epiphytic mosses of the region studied.

2. The federation was *Homomallion adnatum*.

3. Three factors controlled the associations: host tree, topographic position and micro-climate; the element linking each of these being moisture.

4. The various associations, with their substrata and topographic position, were: *Homomallietum adnatum*, *Fagus* and *Acer* on the ridge; *Platygyrietum repens*, *Ulmus* near a field on the ridge, and *Fagus* in the ravine; *Anomodetum tristis*, *Ulmus* within woods on ridge; *Schwetschkeopsetum denticulata*, ravine *Acer*; *Anomodetum*, ravine *Ulmus*; *Leskeetum gracilescens*, lowland *Ulmus*.

5. The associations tentatively arranged in order of increasing moisture requirement would be: *Homomallietum adnatum*, *Platygyrietum repens*, *Anomodetum tristis*, *Schwetschkeopsetum denticulata* and *Anomodetum* (*minor* and *attenuatus*).

6. Bark of all trees tested gave an acid reaction.

7. Bark of different species of trees differed with respect to the absorption of moisture from a saturated atmosphere: *Ulmus* showed the highest absorptive power and *Fagus* the lowest.

8. The moss flora occurring on ridge *Fagus* and ridge *Acer* was limited to two species.

9. *Ulmus* on the ridge had the richest moss flora, with fifteen species present.

10. A different species of moss dominated on each individual tree in the case of ravine *Ulmus*.

11. Four of the eight species of mosses recognized as most representative grew almost exclusively on *Ulmus*.

12. Of the species of epiphytic mosses studied, but two are capable of growing on soil; these two are apparently restricted in their dis-

tribution to silt of dust deposits on the trees, viz., *Amblystegium varium* and *Leskea gracilescens*.

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THE CHROMOSOME RELATIONS OF *SOLIDAGO RIGIDA* AND A GIANT MUTATION

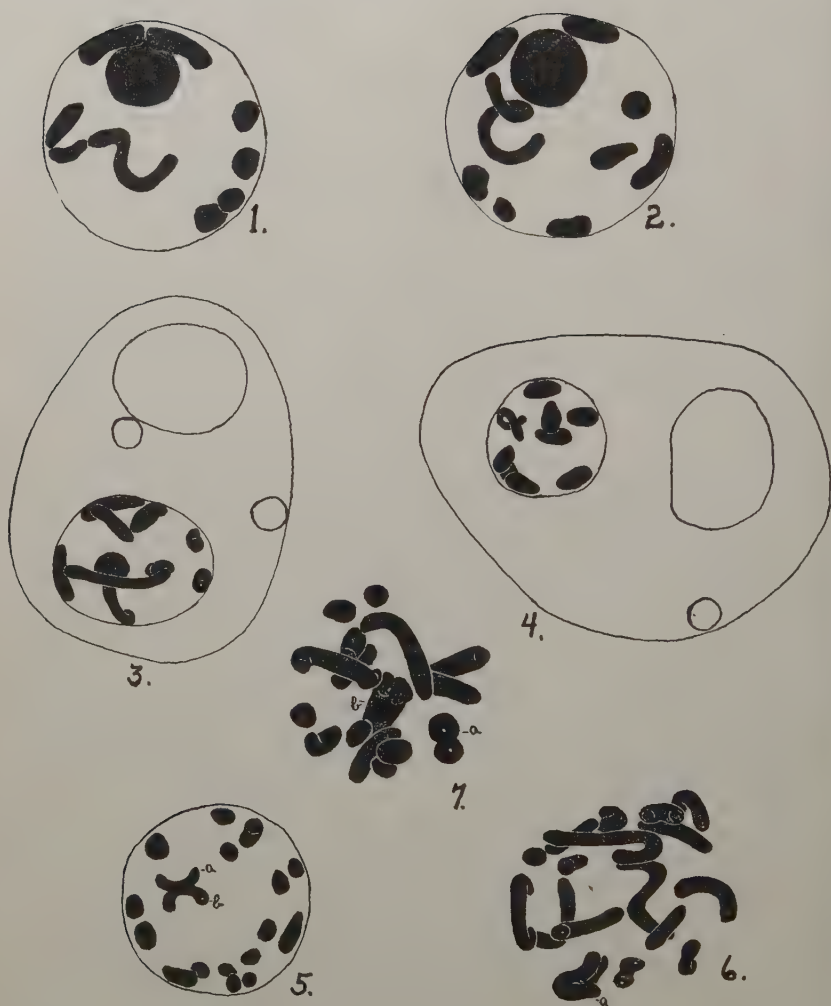
By NOE L. HIGINBOTHAM

During the summer of 1930 an unusual variant race of *Solidago rigida* L. was collected in Newton county, Indiana. This variant was transplanted to the Botanical Garden of Butler University where it has grown since, showing no tendency toward return to the characteristic form of the normal *S. rigida* plants growing in the same plot beside it. The most notable distinctions of this variant are: the larger size, being about twice as high, with larger leaves and flowers; the upper cauline leaves being ovate, obtuse and sessile, with an unequally cordate base; and the later time of blooming, which seems to be due not so much to later initiation as to slower development and maturation of flowers.

The problem as to taxonomic status of the variant naturally arises. The conclusion that it might be a hybrid does not appear likely, because all of its characters appear to be derived from *S. rigida* parents. That the differences are more than mere physiological responses to some environmental factor is evidenced by the fact that they have been maintained when the two kinds of plant are grown under the same condition. To date, nothing has been done to see what its offspring would be. The obviously close relationship of the form to the species makes it unwise to consider it as a new species. Since the differences are chiefly modifications in size, it was thought that the variant might be a gigas-mutation with a tetraploid chromosome complement.

Flower buds of normal *Solidago rigida* and of the variant were collected during the summer of 1934, on August 8 and 17, at the following times: 6:30 a. m., 12:30 p. m., 6:30 p. m. and 12:00 midnight. The buds were left entire and killed and fixed immediately in Nawaschin's fluid. After embedding in paraffin, both longitudinal and transverse sections were made 10 microns in thickness and stained in iron hæmatoxylin differentiated in picric acid, following Tuan's method (4). Observations were made with a Spencer research microscope having a 1.9 apochromatic objective, aplanatic condenser and 20X compensating ocular, giving an initial magnification of 1900 diameters.

Study of the sections revealed comparatively few countable figures, most of the cells being resting pollen mother, dyad or tetrad cells indi-



EXPLANATION: Figures 1, 2, *Solidago rigida*, meiotic prophase. Figures 3, 4, prophase of equational division. Figure 5, *Solidago rigida*, giant variation, somatic prophase. Figure 6, meiotic anaphase. Figure 7, early meiotic anaphase.

cating nearly simultaneous meiotic divisions with a short interphase. This was substantiated by the fact that the size of the chromosomes after the second division appeared to be about half the size of those in the first division. Cells in the same anther were in the same phase in nearly every case, dyads and tetrad both had the same number of chromosomes, and no signs of meiotic irregularity were observed.

Solidago rigida L. (normal). ($x = 9$). Figures 1-4. Both Figures 1 and 2 show 9 bivalent chromosomes in the prophase stage of a pollen mother cell. Both show one chromosome much longer than the rest, four rather short, and four of an intermediate length. This was borne out by focusing for depth, though no exact measurements were made in any case. Figure 3 shows 9 univalents and the nucleolus while in Figure 4 there are 9 univalents but the nucleolus is missing. Both the latter are dyad nuclei. The chromosomes of Figures 1 and 2 are larger than those in 3 and 4. In every case the nuclear membrane was visible.

Solidago rigida L. (giant variation). ($x = 9$). Figures 5-7. Figure 5 shows a somatic nucleus in prophase with 18 (2X) chromosomes. Though chromosome "a" appeared to be partially fused with "b," their relation was interpreted to be only one of proximity. Apparently "a" and "b" are the long chromosomes of the diploid complement. The nuclear membrane was still present. Figure 6 shows 18 univalent chromosomes in the early anaphase of reduction division. The bivalent "a" had not completed disjunction. The nuclear membrane had disappeared. Figure 7 represents an early anaphase, showing 14 univalent and 2 bivalent chromosomes, "a" and "b," which had not completed disjunction. Observations indicated that the long chromosomes were among the first to go to the poles.

Figures 3 and 4 show extra-nuclear bodies which showed staining reaction similar to the chromatin material. They were present in nearly every dyad cell observed but there was nothing to indicate their origin. In many instances the bodies were of irregular sizes and shapes. It is suggested as an hypothesis that the unknown bodies (Figures 3 and 4) may be excluded chromatin material similar to that found in Ginkgo by Shimamura (3). No study was made of this phenomenon.

The chromosome counts agree with those published heretofore for *Solidago* ($x = 9, 18, 27$) (1, 2), indicating a basic number of 9 for the genus. The observations revealed no visible morphological or numerical differences in the chromosome complements of the two forms studied. The variation in stature and other characters noted above apparently is

due to gene mutations rather than duplication of genes. At least, there is no duplication resulting from increased chromosome number. It is possible that a more exact technique would disclose morphological differences in the two chromosome sets but there is no evidence of such differences in the sections studied. It is more logical to conclude the variations to be due to gene mutations (point mutations).

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MODIFICATION OF VASCULAR TISSUE IN MID- VEIN OF QUERCUS ALBA LEAVES INDUCED BY GALL DEVELOPMENT BY CYNIPS PEZOMACHOIDES ERINACEI

By E. FAY KENOYER

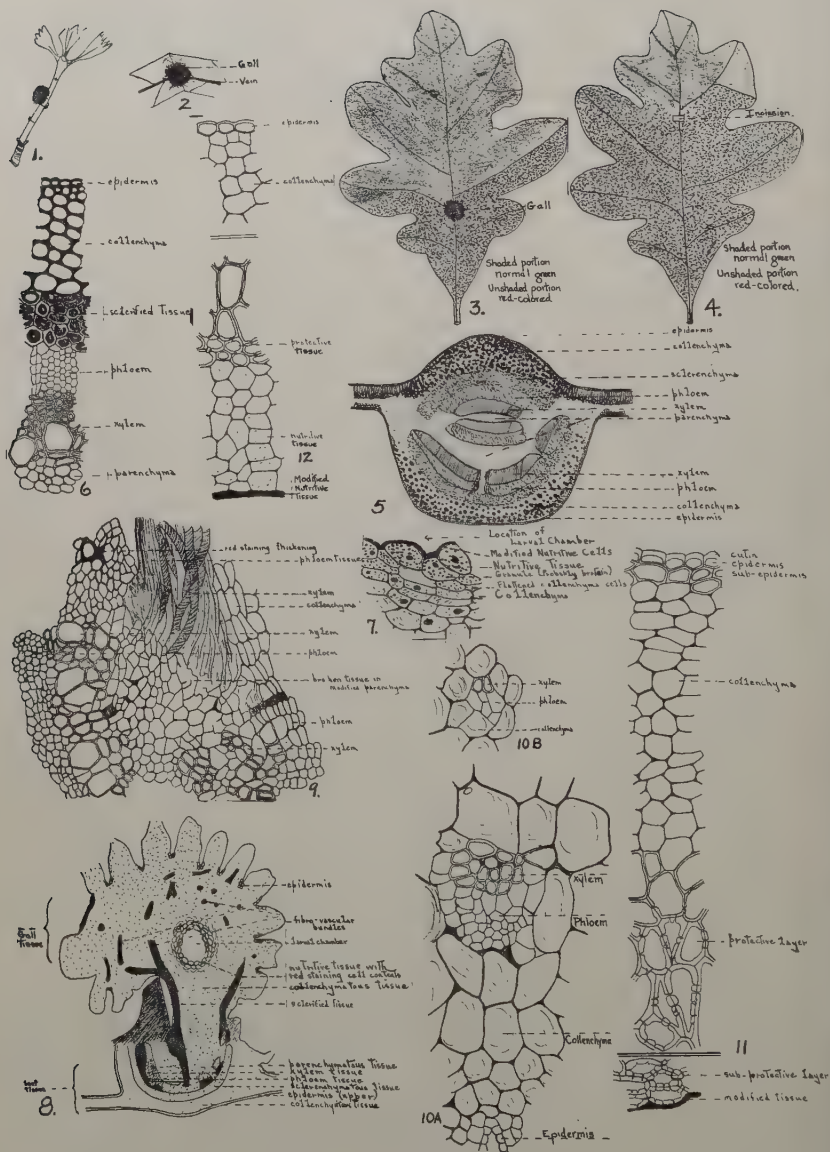
INTRODUCTION

In the autumn of 1933 Miss Agatha Griffin (3) studied the influence of interrupted translocation on loss of chlorophyll in leaves before autumn coloration. During the course of the observation, it was noted that a gall on the vein of leaves of *Quercus alba* produced strikingly similar results as cutting of a vein, *i. e.*, in both cases the area above the cut or gall growth lost its chlorophyll first and turned strikingly red several weeks before the portion below the cut or gall discolored. It was at that time assumed and substantiated by superficial examination that the gall induced some sort of modification in the conducting tissue of the leaf, thus affecting translocation. To investigate the nature of this modification in the vascular tissues is the specific aim of the present study.

METHODS

The gall-infested leaves for this study were gathered at various intervals from the middle of June to the last of October. Specimens were obtained from trees on the Butler University campus, where galls were numerous. When taken to the laboratory, portions were cut from the leaves, each section bearing a gall. About 6-12 mm. of the vein were left on each side of the gall while about 3-6 mm. of the leaf blade were left on each side of the vein.

Five stages were selected for study: (1) Veins showing only ruptures with few trichomes protruding. (2) Galls ranging in size from one to three millimeters. (3) Galls from three to five millimeters. (4) Galls from five millimeters to largest size of about one centimeter on veins showing no indication of brown coloration or modification. (5) Galls on veins which were brown, discolored and displayed modification. The material was killed, some in medium chromo-acetic acid and some in formalin-acetic alcohol.



EXPLANATION OF FIGURES

- Figure 1. Gall of *Cynips pezomachoides erinacei* on a twig of *Quercus alba*.
- Figure 2. Portion of the midvein of a white oak leaf showing the bent surface due to the growth of a gall.
- Figure 3. Leaf of *Quercus alba* showing early red coloration in fall due to gall growth on midrib.
- Figure 4. Leaf of *Quercus alba* showing early red coloration due to cut in midrib.
- Figure 5. Outline drawing of a cross section of the normal vein of a white oak leaf showing arrangement of tissues.
- Figure 6. Detailed drawing showing tissues found in the normal vein of a white oak leaf.
- Figure 7. Detailed drawing of tissue around the larval chamber in stage 1. This tissue is similar in stages 2 and 3.
- Figure 8. Outline drawing of stage 2 showing tissues of gall and vein. Note distribution of vascular tissue in gall, vein tissue pushed to one side of gall, and separation of groups of vascular tissue in vein due to proliferated parenchyma.
- Figure 9. Detailed drawing showing vascular tissue running into gall from leaf vein, tissue of vein, and sclerified tissue pushed to one side of gall growth.
- Figure 10. Cross section of vascular bundle and surrounding tissue in gall: A, large bundle; B, small bundle.
- Figure 11. Detailed drawing showing tissues found in mature gall.
- Figure 12. Tissues found in cross section of gall of *Cynips pezomachoides erinacei* on twig of *Quercus alba*.

When ready for use, dehydration and imbedding in paraffin were carried out according to standard methods. Sections were cut ten microns in thickness. Cross sections of the vein were made in all stages of gall development. The gall was left on the vein in the younger stages while in the older stages it was removed, because of its hardness and consequent difficulty in cutting. Cross sections of the gall itself or cuts longitudinal to the vein were also made. In arranging paraffin ribbons on the slides, serial sections were made. Due to the natural hardness and brittleness of the oak veins and the collapse of cells of the vein in stage 5, it was impossible to make complete serial sections in many cases. Thick cross and longitudinal sections forty to sixty microns in thickness were cut of the mature galls by hand and on the microtome. Twigs bearing galls were killed in formalin-acetic alcohol and imbedded in celloidon. Both cross and longitudinal sections of the twigs were cut on the sliding microtome, thirty microns in thickness. All sections were stained in safranin, counterstained in Delafield's hæmatoxylin, and mounted permanently in balsam.

Amount of vascular tissue in the vein was determined by measuring with the aid of an ocular micrometer around the ring of tissue or across isolated groups of tissue in the gall-infected veins.

OBSERVATIONS

The gall of the agamic wasp, *Cynips pezomachoides erinacei*, is produced most frequently on the midvein of the lower surface of the leaf of *Quercus alba*. It occurs less frequently on the upper surface, and rarely on twigs (Figure 1). It is a spiny or slightly faceted, spherical to oval structure, about one centimeter in length when mature. The galls are a deep red when produced on the upper surface of the leaf, or range from a cream to light red when produced on the lower surface.

After the first galls were noticed on the trees early in July, it was observed that many ruptured places similar to those from which early stages of galls were protruding were present in the veins of leaves. To be sure that these ruptures were caused by *Cynips pezomachoides erinacei*, several leaves were marked for further observation. In all cases, galls of this wasp were later produced in these ruptured places. Veins showing similar ruptures were then collected and designated as developmental stage 1.

Galls developed from these first beginnings to a structure of about

one centimeter in diameter. When gall growth approached this size, it was found in many instances that a pinching of the tissues of the vein occurred beneath the gall (Figure 2). Later brown coloration and modification appeared in such pinched tissue. It was also found that before autumn leaf coloration occurred, the portion of the leaves above gall-growths turned red (Figure 3). A similar reaction was obtained when veins of normal leaves were cut. The portion of the leaf above the incision turned red first (Figure 4). This result is in agreement with those obtained by Griffin (3). It was further observed that frequently the veins of leaves showing this red coloration were brown and discolored with the appearance of disintegration. In many cases disintegration of tissues had gone so far in veins bearing mature galls that the galls fell easily from the leaf.

A histological study of normal as well as abnormal tissue influenced by gall growth is given below:

NORMAL VEIN. The following arrangement of tissues appeared in cross section: Upper epidermis protected by a thick layer of cutin. Beneath this a collenchymatous tissue composed of comparatively thick-walled cells thickened at the corners. Directly below this was a thick-walled, red-staining tissue extending in a ring all around the vein, followed by a ring of phloem enclosing a ring of xylem. A thin-walled parenchymatous tissue lay in the center of the ring of xylem. At the middle of the vein beyond the ring of phloem was also a parenchymatous tissue. Beginning at the lower epidermis, a similar arrangement of tissues was found, except that the phloem and xylem did not form another ring, but extended up on each side of the vein just to the upper ring of vascular tissue (Figures 5, 6).

STAGE 1. Cross sections of a ruptured vein on the lower surface of the leaf showed trichomes about four abreast just developing on the exposed surface of the newly forming gall; yet there had not been any gall tissue visible to the naked eye, nor could it be noticed under a hand lens. The trichomes were composed of slightly elongated cells similar to those composing the remainder of the gall. Epidermal tissue was present. The tissue directly surrounding the larva appeared to be broken down, forming an amorphous, red-staining substance. Outside of this layer were a few rows of large cells containing abundant protoplasm with red-staining granules. Just outside of this were a few rows of small flattened cells. The rest of the newly-formed gall tissue was composed of closely packed collenchyma cells (Figure 7). Orientation of the larval chamber

to the tissue of the vein was determined by comparison with tissue of the normal vein. It was found that the chamber lay chiefly in the xylem tissue, in close contact with the phloem. The central parenchymatous tissue of the vein had been proliferated and contained part of the larval chamber. Vascular tissue found normally in the lower part of the vein had been interrupted by the formation of gall tissue.

STAGE 2. Vascular bundles were present to supply the gall with food and water by the time it had become about 2 mm. in diameter. Figure 9 shows details of the vascular tissue running from the vein into the gall. Marked rearrangement of the tissue of the vein was noted by the time the gall had reached this stage. Vascular tissue was separated and rearranged into various isolated groups, due to proliferation of parenchymatous tissue between the vascular elements (Figure 8). This separation and rearrangement of vascular tissue was common in most of the infected veins studied.

Another source of rearrangement of the tissue of the vein was the proliferation of the tissue near the larval chamber. Parenchyma and vascular tissue proliferated, finally pushing up and out of the vein of the leaf to form the gall. In this process, tissue normally lying over the place in the vein where the egg is deposited, takes up a position to one side of the gall when the gall develops (Figure 9). In many cases a deposit of some brown substance was observed in this tissue pushed to the side of the gall as well as in the leaf blade close to the gall. This may be a tannin deposit; Winton (8) says that tannins are usually associated with brown coloring substances. In many cases this rearranged tissue also had become sclerified and had developed heavy red-staining walls and thickenings (Figure 9).

A study of the gall tissue (Figure 9) showed typical large masses of xylem and phloem running up into the gall. It was found that these vascular elements branched out into the collenchyma when they reached the gall tissue, so that small vascular bundles were obtained, each oriented so that the xylem was toward the center of the gall and the phloem was toward the outside. In size, the bundles ranged from small, containing only one to few xylem elements, to large, containing several xylem elements (Figure 10).

Epidermis, collenchyma and nutritive tissue were similar to that found in stage 1, except that in the pedicel-like structure supporting the gall a centrally-located area composed of cells elongated with their long axis vertical to the leaf blade was noticed. The ends of some of the cells

were at right angles to the sides, while others were oblique or tapering. The walls were somewhat thickened and simple pores were noticeable in the walls.

STAGE 3. Tissues of the vein and gall were similar for the most part to those found in stage 2. Beneath the epidermis was a thick layer of collenchymatous tissue well supplied with vascular strands. The cells enclosed a crystalline substance and prominent large nuclei. Adjoining on the inner side was a layer, a few cells in thickness, which contained large nuclei, as found in the collenchyma, and other smaller irregular bodies staining red with safranin. Inside of this tissue was a broken-down amorphous tissue staining uniformly red throughout.

STAGE 4. A large amount of vascular tissue leading into the gall structure was present. In some instances, even the lower row of vascular tissue in the vein was tapped to supply the gall. The collenchymatous cells below the epidermis of the vein showed signs of collapse in this stage, especially at each side of the vein. This had been noticed in a few of the younger stages after gall-tissue had pushed out of the vein and forced the vein-tissue to each side. Some of the parenchymatous tissue of the vein also showed evidence of disintegration.

STAGE 5. The most striking feature was that most tissue of the vein seemed to be in a state of collapse. In fact, it was very difficult to obtain sections of these stages, because of the brittleness and degeneration of the tissue. A longitudinal section of a mature gall (Figure 11) showed epidermal tissue present. Directly below this was a thin layer of compact red-staining cells having sclerified walls. When material was observed macroscopically, it appeared to be composed of a glistening crystalline layer. Beneath this was a layer of collenchyma which also appeared crystalline, macroscopically. This tissue made up about one-half of the gall growth, and contained only remnants of protoplasm. Beneath this and extending to the larval chamber, was a layer of red-staining sclerenchymatous tissue. This consisted of enormous, very thick-walled, elongated cells containing numerous simple and branching pores extending partially or all the way through the cell wall. There were no large thin-walled cells surrounding the larval chamber as observed in younger stages, but a compact layer of smaller, somewhat flattened yet nearly isodiametric, six-sided sclerenchymatous cells was present.

GALL BORNE ON TWIG. A cross section of a gall formed on a twig showed development similar to that found on the leaf (Figure 12). Proliferating parenchymatous tissue of the pith had pushed some of the

vascular tissue to each side of the gall growth. The cells of the pith had undergone a peculiar change. Those opposite the gall had become sclerified, while in the center of the twig was a deposit of a dark heavily-staining substance. Then toward the gall from this deposit were the ordinary, only slightly larger, pith elements.

VASCULAR TISSUE OF VEIN INTERRUPTED BY GALL GROWTH

It was found that the amount of vascular tissue present in a section through a gall-infected vein did not equal the amount found in the normal vein. It was also seen that this was caused by interruption of the vascular tissue by gall-growth. Reference to Table I gives some idea of the amount of such interrupted vascular tissue.

TABLE I
SHOWING INTERRUPTED VASCULAR TISSUE DUE TO
GALL GROWTH IN VEIN

Surface of leaf bearing gall	Vascular tissue in normal leaf. Lineal microns	Vascular tissue left in gall- infected leaf. Lineal microns	Amount of vascular tissue interrupted. Lineal microns	Percentage of vascular tissue interrupted
Upper	1696	1431	265	15.6
Upper	2014	1484	530	26.3
Upper	1802	1590	212	11.7
Upper	1908	1484	424	22.2
Upper	1908	1484	424	22.2
Lower	1696	636	1060	62.5
Lower	1908	1272	636	33.3

The average loss of vascular tissue due to interruption by gall growth in the vein when galls were produced on the upper surface of the leaf was 27.7 per cent. In most cases, only the upper part of the ring of vascular tissue found normally in the upper part of the vein was affected. When galls were produced on the lower surface, however, it was found that more tissue had been interrupted. Not only had part of the row of vascular tissue extending around the lower part of the vein been affected, but also the lower portion of the ring of vascular tissue found in the upper part of the leaf had been interrupted. In one case, only the phloem of the lower portion of the ring was affected, leaving the xylem unaffected.

DISCUSSION

In a description by Kinsey (4) of the tissues found in galls belonging to Cynips, the following tissues are recognized: *Epidermal layer*: outer covering of gall with peculiar faceted surface in many species. *Spongy parenchyma*: occupying the central portion and constituting the major portion of material in all spongy and more hollow oak apples of this genus. Poorly developed in the subgenus Antron and absent, as far as he could see, from the galls of the subgenus Acraspis. *Protective zone*: apparently absent in Acraspis—sclerified tissue. *Collenchyma*: lying directly beneath the epidermis. A second layer in which the cells have thickened walls and usually crystalline contents—bulk of material in Acraspis. *Nutritive layer*: innermost tissue of the gall, lining the larval cell. A distinct layer in young galls of many species, soon becoming reduced by the feeding of the larval insect (and probably by absorption by other plant tissues) to a thin, broken layer of partially empty cells. Poorly developed in any but the very youngest gall of Acraspis. Possibly directly descended from phloem.

In the present investigation the following tissues were recognized: *Epidermis*: tissue covering the outside of the gall and becoming heavily cutinized in older stages (Figure 11). *Subepidermal layer*: present only in mature gall. Consists of a layer only a few cells deep, sclerified, having a thick wall and occasional pores (Figure 11). *Collenchyma*: found under above layers. Comprises the major portion of gall. It consists of nearly isodiametric to elongated cells, having deeply-staining walls thickened a trifle more at the angles than elsewhere. In young stages it contains abundant protoplasm with large nuclei; later, crystals develop and finally only remnants of cell contents are left (Figures 7, 11). *Nutritive zone*: lining larval chamber in young galls; composed of large, loosely associated cells of parenchymatous character, and containing abundant protoplasm with red-staining granules, probably protein (Figure 7). *Protective zone*: In mature galls, this tissue is found inside the collenchyma. It is a very heavy-walled, sclerified tissue, having enormous simple or branched pores extending partially or all the way through the cell wall (Figure 11). *Subprotective zone*: In the mature galls there is a thin layer a few cells in thickness instead of a large-celled area surrounding the larval chamber. This consists also of sclerified cells with wall pores, but they are not radially elongated. These are more nearly isodiametric.

Since *Cynips pezomachoides erinacci* belongs to the subgenus Acras-

pis, it may be seen that the present data differ from those given by Kinsey in two essential places, (1) the presence of a subepidermal layer of sclerenchyma and (2) the presence of an inner sclerified layer below the collenchyma, consisting of radially elongated cells of a protective zone, and more nearly isodiametric cells of a subprotective zone. There are two explanations for such a difference. Either younger stages of the gall were used for observations in the former report or there are variations in the structure of this gall and the structure of other galls of this species, so that the wasp, *Cynips pezomachoides erinacei*, may produce galls either with or without the subepidermal and protective zones.

The occurrence of the gall of *Cynips pezomachoides erinacei* on the twig as well as on the leaf is "rare, although not unknown," according to Kinsey. Several such galls were noticed during collection of material.

Insertion of the egg into the central portion of the vein in contact with xylem and phloem tissue is in accordance with the description by Beyerinck. Orientation of the vascular bundles in the gall tissue (Figure 10) with the xylem inside and the phloem outside was found to correspond with that described by Küster (6) for the normal gall. Exceptions are numerous, however, according to him. Distribution of the vascular tissue through the gall seemed to indicate that some of the strands might form a closed network, for in some sections it was found that the vascular tissue was continuous up each side of the gall and almost met in the center. The presence of very small vascular bundles, seen in a cross section of the gall, would indicate a system similar to that found in the leaf in which the bundles finally end in minute branches consisting of only one xylem vessel and few phloem cells. Few vascular elements were also found extending out into the trichomes (Figure 8).

According to several investigators, the enlargement of the cells of the nutritive zone is due to the storage of abundant food substances. It was noted that cells surrounding the larval chamber contained large red-staining granules. This has been noted by Kostoff and Kendall (4), who point out the accumulation of food material in various types of tissues where foreign substances are introduced into the living tissue.

Cosens (1) attributes the accumulation of food at the source of irritation to another cause: "Summing briefly, the larva secretes an enzyme capable of changing starch to sugar, which acts on the starchy constituents of the nutritive zone and accelerates the rate of their change to sugar. The material thus prepared supplies nourishment for both the larva and gall. The protoplasm of the latter is thus rendered unusually

active, since it receives an abnormal quantity of available food material in a limited area. The hypertrophy and cell proliferation and probably also the appearance of vestigial tissue or other primary characters are the response of the protoplasm of the host to the additional food supply." Weidel (7) postulates that chewing by the larva causes development of the protective tissue from the starch parenchyma, and development of the nutritive tissue from the protective tissue in *Andricus globuli*.

Esau (2), in working with the curly top virus in sugar beets, found interesting stages during the infection. First, the process begins with the development of giant cells. These arise from phloem parenchyma or pericycle cells adjacent to the first normal sieve tubes. Primary hypertrophy usually accompanies the hyperplasia manifesting itself in the phloem or pericycle cells farther removed from the sieve tubes. This may, however, fail to take place. There is then primary necrosis or death of giant cells. In the second stage, secondary necrosis, the giant cells collapse. These cells die, probably because they have developed abnormally and do not function as healthy cells. In secondary hypertrophy and hyperplasia, phloem parenchyma cells are proliferated around the collapsed cells. They commonly occur in plants when cells are injured or dead. "Resembling wound repair reactions, they do not require the presence of a specific infection to explain their occurrence."

These conceptions of the accumulation of nutritive material around the larval chamber offer a partial explanation of data recorded. Due to an irritation, either by the chewing of the larva, a secretion of an enzyme, or both, the parenchyma of the vein is stimulated to produce large cells closely surrounding the source of irritation, the egg and later the larva. Cells farther removed from the source of irritation, or vascular tissue, are also stimulated to proliferation and a gall-growth results. By enzymatic action or the chewing of the larva, cells of the nutritive tissue are degenerated and are seen as amorphous, broken-down tissue lining the larval cavity. In older stages, the entire disappearance of the nutritive zone and the production of the protective tissue, seen first as a row of heavy-walled cells and then as a thick layer of tissue surrounding the larval chamber, may be, as suggested by other investigators, a natural reaction of the plant toward a source of irritation.

The abnormal rearrangement of the tissue of the vein by parenchymatous proliferation as well as the pushing of the vein tissue to the side as the gall pushes through the epidermis of the vein, offer evidence for an explanation of the disintegration of the tissue as noted in veins bear-

ing galls of late stages. The general straining of tissue caused by such development would naturally stretch some cells and crush others, so that, under such abnormal conditions, cells would tend to die and disintegrate. Thus, the vein beneath the mature gall is found to be brittle and disintegrated, in many cases resulting in interrupted translocation.

Although there was interruption by gall growth in approximately 20 per cent of the vascular tissue of the vein in galls borne on the upper surface of the leaf, and from 33 to 62 per cent in veins bearing galls on the lower surface, it is not thought that this interruption is sufficient to be the cause for early red coloration in gall-infected leaves. Interruption of the vascular tissue of the vein is seen in early stages of gall development. However, it is not until later in the summer that red coloration in the leaf is apparent. Degeneration and collapse of cells in the vein caused by the death of the strained tissue increases as late summer approaches. Thus, it is thought that the collapse of the strained tissue is evidently the chief cause of the brown coloration of the veins and results in early red coloration in the leaf.

CONCLUSIONS

1. Early red coloration in the autumn leaves of *Quercus alba* above the growth of a gall of *Cynips pezomachoides erinacei* is evidently due to interference in the translocation channels in such leaves.

2. Partial interference is apparently caused by: (a) Deflection into the gall of about 20 per cent of the vascular tissue of the vein on leaves bearing galls on the upper surface, and 33 to 62 per cent in veins of leaves bearing galls on the lower surface. (b) Deflection of vascular tissue of the vein into the gall where it branches in a partially open network prevents the normal translocation of food, water and minerals to the tip of the leaf.

3. The chief interference is caused, however, by the collapse of cells in the vein, due to the strain on these tissues as a result of hyperplasia, hypertrophy and consequent gall growth.

4. The young gall of *Cynips pezomachoides erinacei* is differentiated into epidermis, collenchyma and nutritive tissue.

5. The mature gall is differentiated into epidermis, subepidermis, collenchyma, protective zone and subprotective zone.

6. Galls of this species are found on the stem of *Quercus alba* as well as on the leaves.

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STRATIGRAPHY AND PRELIMINARY POLLEN ANALYSIS OF A LAKE COUNTY, ILLINOIS, BOG¹

By RUSSELL C. ARTIST

The last decade has marked a growing interest in paleoecology stimulated by stratigraphic studies and pollen analyses of peat deposits. A number of bogs of considerable interest occur in the northeastern part of the state of Illinois, in Lake and McHenry counties (Waterman 10).

In the fall of 1932 a detailed study of one of these bogs, the deposit about two miles north of the town of Volo, Illinois, was begun. This occurs in the Gray's Lake Quadrangle, whose exact boundaries are $42^{\circ} 15' - 42^{\circ} 30'$. The investigations followed two main lines: (1) Analysis of the fossil pollen grains in the peat to determine the possible changes in the vegetation of the region which have taken place during the formation of the bog, and (2) Microscopic analysis of the peat to determine the botanical composition of the various peat-types occurring as well-marked strata in the deposit. Much information concerning the history of the development of the bog can be obtained from a knowledge of the peat profile.

METHODS

The methods employed here are essentially those used by Erdtman (3). Samples of peat were collected at intervals of twenty centimeters from the surface to the bottom of the bog. Complete series of samples could only be taken in sections of the bog where the peat was firm enough to be cut and retained by the sampler. A portion of the center of the core was carefully removed with a scalpel and placed in numbered glass vials. They were brought into the laboratory and prepared for study while still moist.

Approximately one cubic centimeter of material was boiled in 10 per cent potassium hydroxide to which a few drops of safranin had been added, centrifuged, decanted, washed with distilled water, centrifuged and decanted again. A small amount of the material near the surface of the filtrate was removed by means of a pipette and placed on

¹A portion of the work done on a thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Northwestern University. The pages of Butler University Botanical Studies are open to all Butler University alumni.

a slide. After most of the water had evaporated, glycerine and cover slip were added. Permanent slides were ringed with balsam and at least two slides from each level were prepared.

Erdtman (3) and Sears (8) claim that trustworthy results are obtainable by counting 100 or 150 pollen grains per level. The latter number was used in all the counts in this study. Identification was made on the basis of measurements of extant pollen grains of identical genera and comparison with Sears' (8) drawings and descriptive key. As specimens of pollen of present-day plants were not available in sufficient amounts to make accurate identification of all fossil pollen possible, a comparison was made of the proportions of pollen of winged conifers and of deciduous trees and herbaceous plants at the different levels in the peat. Winged coniferous pollen was further differentiated as to the genera: *Abies*, *Picea* and *Pinus*. Results of the tabulation are shown in Figure 2.

OBSERVATIONS

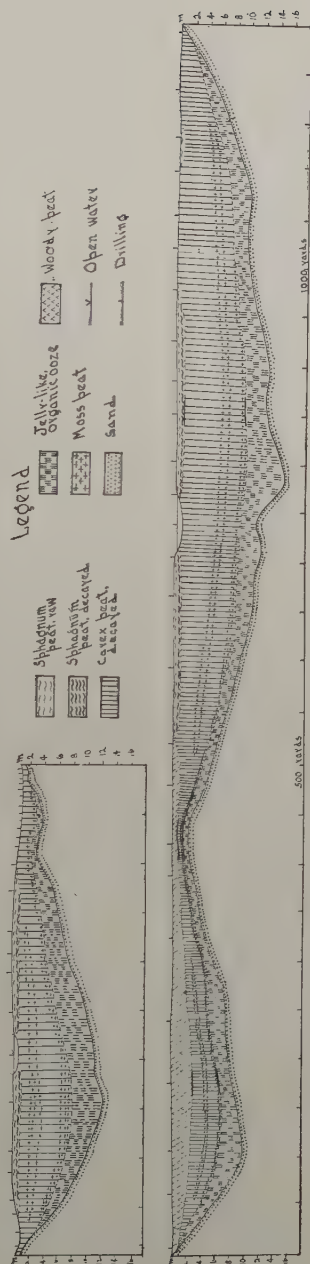
The following peat-types were found from the top downward: *Raw Sphagnum peat*: less than 5 cm. thick, consisting of the dead lower parts of living plants and only fairly well preserved. *Decayed Sphagnum peat*: about 15 cm. in thickness, in all stages of decomposition. This depth of *Sphagnum peat* is not in accord with the previous report of about seven feet given by Kurz (6). *Carex peat*: from 2.0-2.5 m. thick, finely fibrous, dark brown, consisting mainly of rootlets, grass stems, some woody fragments and parts of free vascular strands; much decayed. *Moss peat*: 1.0 m. in average thickness, reddish brown, coarsely fibrous, composed of a single species of an aquatic moss, *Drepanocladus Wilsoni Schimp.*, a common bog and lake moss both in Europe and North America.¹ It is intermixed with fine rootlets. *Carex peat*: 1.0 m. thick, finely fibrous, dark brown, containing seeds, stems of grasses and parts of leaves. Moss stems in the lower portion. *Moss peat*: 2.0 m. in thickness, coarsely fibrous, dark brown to black, consisting of *Drepanocladus Wilsoni Schimp.*; larger and blacker than the same species in the moss layer above. Williams² states that the species of this genus are all quite variable and that the larger and blacker specimens of this layer grew more submerged in water than the others. *Organic ooze*: 1.2 m. thick, gray brown, jelly-like and rubbery, amorphous, with only

¹Specimens of mosses sent to Dr. R. S. Williams for identification.

²Personal communication.

FIGURE 1

Bog Profile, Constructed from Both Lengthwise and Crosswise Lines of Drilling, Volo Bog



a few fibrous strands in the upper portion. Incineration shows it to be largely organic matter with little mineral residue. In a few cases it contains shells of molluscs. This layer rests upon a sand bottom.

The peat-types described above are in the same sequence throughout the bog, though in varying amounts. In the extreme northern and southern parts of the bog the Sphagnum peat is absent and the Carex peat is overlain by dry woody peat 1.0-2.0 m. in thickness, very coarsely fibrous, red brown, consisting of branches and roots of trees and small stems of shrubs. Figure 1 illustrates profiles of the bog constructed from both lengthwise and crosswise lines of drillings.

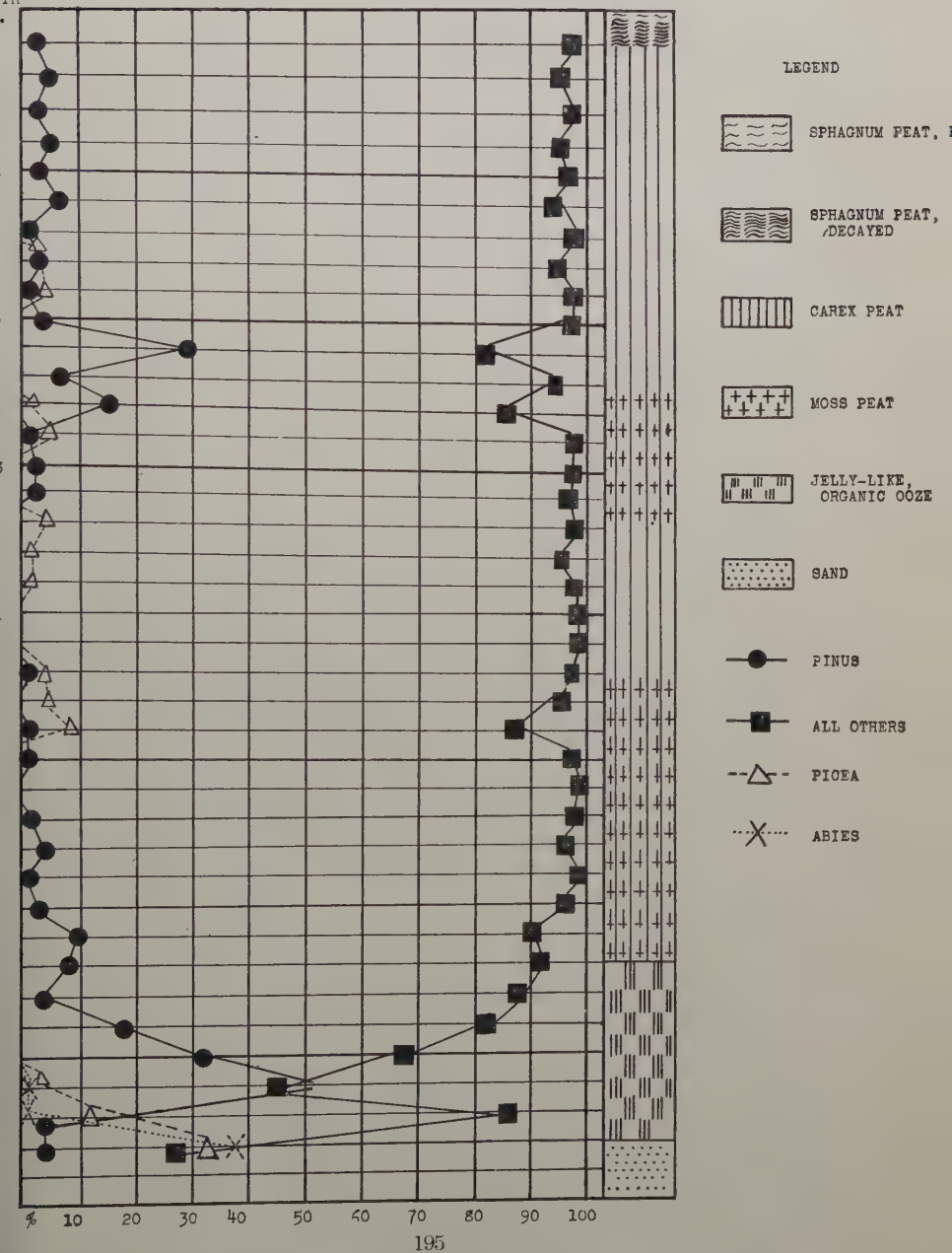
In one or two instances, deposits of marl were encountered, 1.0-1.2 m. in average thickness. Where marl is found, it occurs as a layer above the sand bottom or is incorporated with the organic ooze. This was particularly true at the point where the bottom rises to within two meters of the surface. The following molluscs taken from the marl were identified by Dr. F. C. Baker: *Valvata tricarinata* (Say), *Amnicola Leightoni* F. C. Baker, *Amnicola gelida* F. C. Baker, *Fossaria obrussa decampi* (Streng), *Gyraulus* sp. undet., *Physsa sayii* Tappan, immature. According to Dr. Baker, both species of *Amnicola* are not found living at present, and *Fossaria* is approaching extinction. However, all are molluscs that lived in fresh water.

A summation of total number of spores counted and the relative per cent of each kind shows that where percentage of conifer pollen is high, there is a correspondingly low percentage of deciduous pollen. The analysis graph and bog profile (Figure 2) show that *Abies* and *Picea* are dominant at the lowest level, deposited in vast quantity at an early stage of the bog-lake when its surface was not covered by vegetation. Above this the peat consists of organic ooze or material deposited under water, of moss peat, *Carex* peat, moss peat again, *Carex* peat again and Sphagnum peat in the order named. From the 6.4 m. to the 0.2 m. level the peat represents material deposited in shallow water or from the underside of floating vegetation mats. In this portion of the profile, *Pinus* pollen appears only in minimum quantity, whereas deciduous pollen is dominant. *Abies* pollen disappears entirely above the 7.0 m. level, while *Picea* pollen appears at four disconnected levels, viz., at 4.4-4.8 m., 3.4-3.8 m., 2.6-2.8 m., and 1.4-1.8 m.

FIGURE 2

POLLEN DIAGRAM AND BOG PROFILE, VOLO BOG

TH



DISCUSSION

As the diagram indicates, a conifer forest of *Abies* and *Picea*, no longer present in this region, controlled the area during the early development of the bog, but was later replaced by a deciduous forest which has remained dominant up to the present time. The sudden change from coniferous pollen dominance to deciduous pollen dominance suggests that the factors unfavorable to the then dominant forest aided the invaders in rapid ecesis. Distribution of vegetation is dependent upon climatic conditions, and, according to Auer (1), "the pollen content of the successive layers of the individual bogs is a direct indication of the comparative abundance of the different trees growing at the time the peat layers were forming." This succession of trees is typical for the majority of bogs in southeastern Canada (Auer (1)), in Wisconsin, Michigan and Ohio (Sears (8)), Illinois (Voss (9)), and Indiana (Lindsey (7) and Houdek (5)). Bogs of Indiana and Illinois (Lindsey (7), Houdek (5), Voss (9), and Fuller (4)) show *Abies* disappearing in the lower strata, as is shown in the present study of the Volo bog. *Picea* usually persists only for a short time after the disappearance of *Abies*. Farther north in Wisconsin (Fuller (4)), *Picea* persists throughout the entire postglacial period. The behavior of *Picea* in the present study is thus intermediate between that shown farther south in Illinois and Indiana (Voss (9) and Lindsey (7)) and that farther north in Wisconsin.

As to climatic changes, predominance of pollen of *Abies* and *Picea* is generally thought to indicate a cool, dry climate, and predominance of pollen of deciduous trees and herbaceous plants a warmer, more humid climate. The presence of decayed peat layers is thought by Dachnowski (2) to indicate a change in climate, but he suggests that this correlation needs further investigation. The primary conclusions drawn from most of the investigations in this field have been concerning climatic changes as reflected in the relative pollen abundance. However, except for the apparent change to warmer and dryer conditions immediately following the melting of the ice, generally regarded as a definite change in climate, the limited scope of this paper prevents any broader interpretation of climatic change.

Whether or not the data presented indicate climatic changes since the Late Middle Wisconsin ice invasion, they at least show the succession of vegetation since that time. The order of postglacial succession has been: *Abies-Picea*, *Picea-Pinus* and *Pinus*-all others.

SUMMARY

1. The Volo bog is a water-laid peat deposit which has formed in a depression containing two basins. The shallow basin is completely filled with solid peat, while over the deeper basin a small body of open water still remains. The depression is found in highly calcareous till of Late Middle Wisconsin age.

2. Two main layers of peat occur in the deposit: (1) Organic ooze, the lower one-fourth, and (2) *Carex* peat, composing the upper three-fourths of the total depth of peat. In this deep stratum there occur at two levels distinct layers of moss peat of a single species of an aquatic moss, *Drepanocladus Wilsoni* Schimp.

3. There is no *Sphagnum* peat recognizable as such below a depth of twenty centimeters in the Volo bog. There is a gradual transition downward from living *Sphagnum* at the surface to *Sphagnum* which is greatly decomposed and finally entirely absent. The disintegration and decomposition of the *Sphagnum* as well as much of the *Carex* peat is apparently associated with extensive bacterial action in the alkaline water and with periods during which the bog was not submerged.

4. Pollen of *Abies* and *Picea* reach a maximum in the lower levels, followed by an increase in pollen of deciduous trees and herbaceous plants. *Pinus* pollen continues throughout postglacial time. This indicates that the depression at Volo began filling up at a time when a conifer forest dominated the area, but which was soon replaced by a deciduous forest which has remained dominant up to the present time.

5. The stratigraphy may or may not indicate climatic changes during the postglacial period, but the pollen analysis shows that the order of succession since the last ice invasion has been: *Abies-Picea*, *Picea-Pinus* and *Pinus*-all others.

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THE EFFECT OF PRECIPITATION AND TEMPERATURE ON ANNULAR-RING GROWTH IN FOUR SPECIES OF QUERCUS

By ARNOLD KLEINE, JOHN E. POTZGER and RAY C. FRIESNER

Of all the factors affecting growth in trees, precipitation and temperature appear to be the most readily measurable, though there is by no means a general agreement among workers as to the exact way in which the relationship is expressed. Pearson (5) found that spring precipitation (April and May) is the most obvious controlling factor in annual height growth in *Pinus ponderosa* saplings. Stewart (7), however, in comparing widths of annular rings of an oak stump with precipitation records taken at Rochester, New York, twenty-five miles farther north, found that there was a greater correspondence between precipitation for June and July and the ring width than for the entire year. Robbins (6), at Columbia, Missouri, measured the growth rings of sixteen oak stumps, and found that the mean monthly temperature of May and June varies inversely with annual increase in tree width. He also found there is a close relation between the total rainfall of March through June and the annular ring width. Diller (2), working on *Fagus*, found that yearly variations in the width of annular rings are correlated inversely with the average temperature for the month of June; also that yearly variations are correlated directly in certain woodlands with the total precipitation for the month of June.

Robbins (6) states that an abnormally large or small annual precipitation shows its effect on the ring width the following year, and that the dry spring of a given year shows its effect in growth during the same year. Diller found that, in most cases, drought years show their effects on growth the following year, probably due to an accumulated deficiency in soil moisture, whereas wet years show an increase in growth the same year. Lodewich (4), while investigating the relationship between certain climatic factors and diameter growth in longleaf pine in western Florida, found no effect of temperature on wood production, but a marked reduction or increase in precipitation was accompanied in most cases by corresponding variations in ring width.

Robbins (6) states that the sums of the mean temperature for certain months have been found to vary inversely with growth, while Diller

(2), working with *Fagus*, found that the mean temperature of the month of June exhibits the same inverse relation.

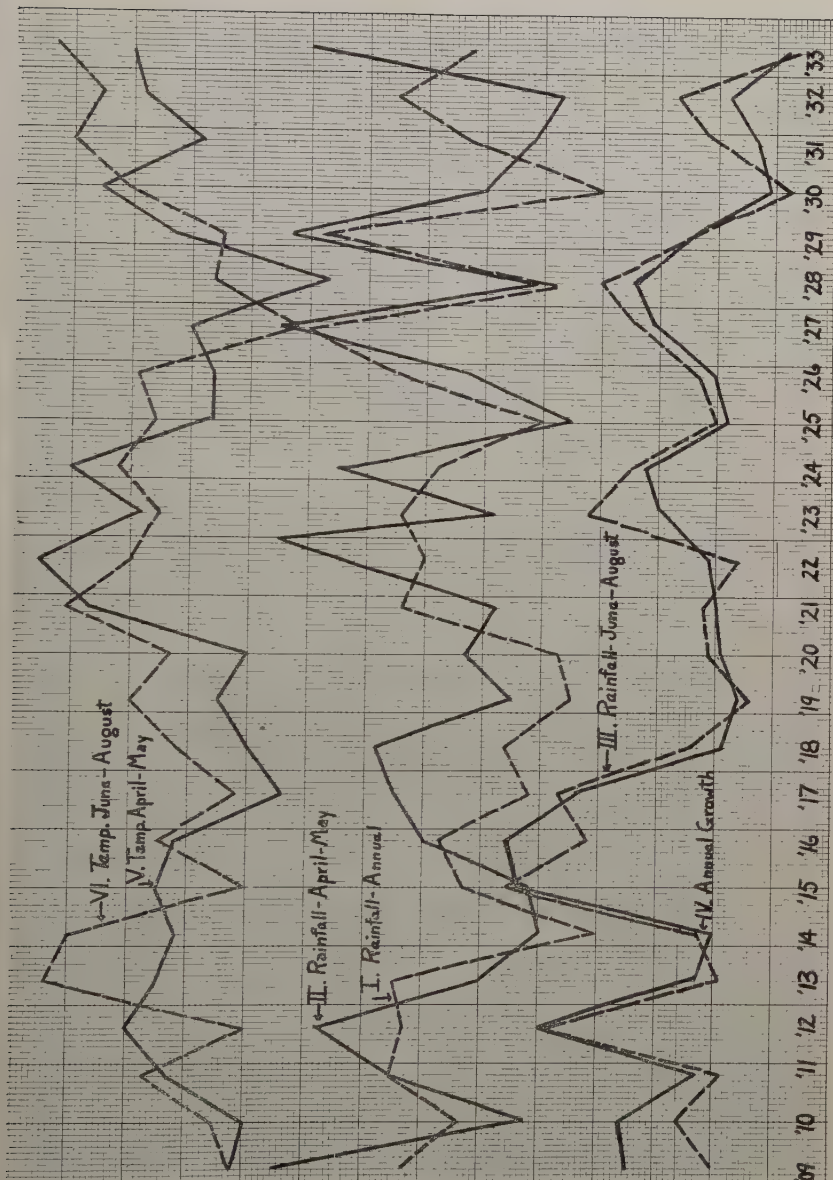
Douglass (3) suggests the possibility of a correlation between sun spots and ring development. Burns (1), in his study of the relation of rainfall and width of annual rings in a Vermont forest, goes so far as to say that there can be no direct correlation between rainfall and diameter growth, because the width of rings at any one point is not an index to total increment, and soil moisture is not a measure of rainfall nor of food supply.

METHODS AND MATERIALS

The present investigations were made from 11 trees of *Quercus alba*, 17 trees of *Q. montana*, 16 trees of *Q. velutina* and 9 of *Q. borealis maxima*. All specimens were taken from the knobs area of Bartholomew and Brown counties in Indiana, from stumps left by lumbering operations carried on from July to September, 1934. Sections were brought to the laboratory and measurements were made with a binocular microscope suspended over the section. The annular ring widths of eight equidistant radii were taken on each of the 53 sections measured. During the measuring, medullary rays were followed instead of geometrical radii. In this manner the width of the annular growth was taken in a direction eliminating the error of oblique measurement. When a radius was completed, a number tag was placed at the end of the radius. This allowed for a recheck to be made at any desirable time. Annular ring measurements were taken of the years 1909-1933 inclusive, a growth period of twenty-five years. The measurement of eight radii per section aided in eliminating the errors of unequal growth along different radii in the same tree.

OBSERVATIONS AND RESULTS

The most outstanding feature at first noticed in the data is the large amount of ring growth in 1912. Then for the years 1913 and 1914 there is a great decrease in annular growth, and in 1915, 1916 and 1917 there is an enormous amount of growth again. This may readily be observed in Curve IV. Since all 53 trees possessed this same characteristic growth between 1912-1917, it is of vital importance to know the relation that precipitation and temperature have during this same time. Rainfall and temperature data were taken from the U. S. Weather



Bureau stationed at Columbus, Indiana, which is ten miles east of the area from which the tree sections were taken. The average monthly precipitation for the summer (Curve III) months of June, July and August shows almost identically the same curve as the ring growth. Also in Curves II and IV it is observed that there is little correlation between the average ring growth and the average monthly precipitation for the spring months of April and May or the total annual precipitation shown in Curve I.

In making a comparison of the ring growth for the other nineteen years (the years 1909-1933, excluding 1912-1917, inclusive), it is found that the same results are obtained as with the period 1912-1917. It almost invariably happens that when there is an increase in precipitation during the months of June, July and August for a certain year, there is an increase in the annular growth for the same year. This correlation follows so closely that when the precipitation curve for a particular year goes above or below the average line (Curves III and IV), the annular growth curve generally crosses the average line at the same time.

In a general way, both the average monthly precipitation curve for spring and the total annual precipitation curve correspond with the curve for annular growth. During the years 1914, 1919, 1920, 1925 and 1930 there was the least total annual precipitation. Both the spring and summer precipitations are low during these years, and, as a result, all of these years have a small amount of annular growth. Thus these results do not seem to agree with those of Diller (2), who held that drought years show their effect the following year. From the results of the present investigation, it appears that whether low total annual precipitation is reflected in the growth of the following year depends upon when during the year the drought actually occurred.

In 1919 and 1928 there was a comparatively low annual precipitation, but in both of these years there was a relatively high summer precipitation, and, as a result, there was a corresponding large amount of ring growth. The years 1913, 1927 and 1929 have the highest annual precipitation of the period of years concerned in this investigation, but the growth is not appreciably accelerated, since the average summer precipitation is not heavy during these years.

In making a comparison of the annual ring widths with temperature, it is evident from Curves IV, V and VI that the best correlation occurs between diameter growth and temperature during the months of June,

July and August. However, this relationship is different from the precipitation relationship in that the temperatures are correlated inversely with the ring growth. The higher the temperatures of the summer months, the lower the growth, and *vice versa*. In making a comparison of the relation of summer temperature and summer precipitation to annular growth, it appears that there is not such a definite correlation between the summer temperature and the ring growth as between the summer precipitation and the ring growth. However, the summer temperature is correlated inversely more to the ring width than the spring or annual precipitation is correlated directly to the ring width. There is very little if any correlation between the average monthly temperature of April and May and the annular ring growth. In 1931 and 1932 there is a relatively high summer rainfall, but it was very hot during these two years and as a result small amount of growth occurred.

DISCUSSION

The characteristic growth during the period of 1912-1917, inclusive, was so obvious in all trees studied that when the measurements of a section were taken for this period, it could easily be distinguished just what year was being measured. In several instances mistakes were made in measuring; that is, measurements of a certain year were being recorded for the year ahead or the year behind. However, when measurements came to the years 1912-1917, the mistake was readily perceived and a recheck was immediately started. As a result, it is certain that no error is involved in the data from the standpoint of measurements being recorded for the wrong years.

The question might be asked as to why the particular summer months of June, July and August, rather than any others, should show this relation. Diller (2) holds that June is the important month from the standpoint of precipitation, while other workers have designated other combinations of months. When a comparison is made between the June precipitation and the ring growth, a correlation is found, but it does not correspond nearly so well to the ring growth as do the months of June, July and August. The same is true when June and July are combined, but the correlation is a little closer here than when the month of June alone is used. The inverse relation between growth and temperature probably may be explained by assuming that increased temperature increases the transpiration, and when soil moisture is near the critical

point it results in the same effect as a lower water supply. As mentioned above, in 1931 and 1932 there was a relatively high summer precipitation, but it was also very hot during these summers and a small amount of growth results even though rainfall was higher. Thus, high temperature, due to its effect upon transpiration, may partially nullify the beneficial effect of a high rainfall. In this connection, attention should be called to the physiography of the area from which the wood sections were taken. All were taken from the Knobs area in which run-off is always high and soil moisture is always near the critical point during summer months. Observations made weekly during the summer of 1934 showed that soil moisture was below the wilting coefficient for six of the thirteen weeks during June, July and August. It is quite likely that in an area where run-off is not so high and where soil moisture is not so near the critical point, the relation between rainfall and growth will be different from that found in this study. It is, therefore, considered that rainfall-growth relations will always be conditioned by the peculiar circumstances pertaining in the particular area under consideration. When there is present low precipitation or low moisture supply, together with high temperature, the limited growth is due to the close relationship which exists between turgidity and growth.

It is known, of course, that precipitation and temperature are not the only factors that have an effect on the growth of trees. Such factors as intensity and duration of light available, mineral salts, and other edaphic factors would enter in. These factors, however, are not so variable from year to year and hence probably do not play so much of a role in the yearly variations in ring development as do precipitation and temperature.

SUMMARY AND CONCLUSIONS

1. Widths of annual rings for 1909-1933 are found to correlate directly with average monthly precipitation during June, July and August.
2. Widths of annual rings for 1909-1933 are found to correlate inversely with the average monthly temperature of June, July and August.
3. The curve for the average monthly precipitation follows the curve of annual ring growth much more closely than does the curve of the average monthly temperature for June, July and August, thus showing that precipitation plays the primary role of limiting factor in annual ring growth.

4. The average monthly spring temperature of April and May has little if any correlation to the annual ring growth.

5. Average monthly precipitation for April and May shows only a slight correlation to annual growth.

6. To some extent, high temperature has the same effect as low precipitation, because of its effect on the increase of transpiration.

7. A low total annual precipitation causes a decrease in annual ring growth only when spring and summer precipitation is low. Thus, drought years in the area here studied show their effects on growth the same year of the drought.

8. The optimum condition for growth is a cool temperature with a high precipitation during June, July and August.

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SOIL MOISTURE AND THE NATURE OF THE TSGUA AND TSUGA-PINUS FOREST ASSOCIATIONS IN INDIANA

By RAY C. FRIESNER and JOHN E. POTZGER

Nichols (6) concludes that "white pine, throughout a large part of its geographical range, is a normal, although minor, constituent of the climatic climax forest." He maintains that the *Tsuga-Pinus strobus* region is a distinct ecological unit which is the climatic climax for the region where they occur. Most universally associated with these species are *Fagus grandifolia*, *Acer saccharum* and *A. nigrum*, and, in lesser proportions, a considerable number of additional species are often found.

While the distribution and commingling of these five species (*i. e.*, *Tsuga canadensis*, *Pinus strobus*, *Fagus grandifolia*, *Acer saccharum* and *A. nigrum*) in the Appalachian, New England and northern Lakes regions is such as to appear to fully justify this treatment in these areas, the distribution in Indiana is such (4, 5) that it is less reasonable to consider them as members of the same ecological unit. *Tsuga* and *Pinus* not only have a very disjunct distribution in the state, but always occur under more xerophytic conditions than do *Fagus* and *Acer*. It would appear more reasonable under such conditions to think of them in Indiana as more xerophytic relict segregates of a former less differentiated climax. That is to say, former climatic conditions may have been such as to favor a less differentiated forest climax (Braun (1)) and, as climate has changed, this climatic aggregate has become segregated into component parts of which *Fagus-Acer* and *Quercus-Carya* are the only ones prominently represented in Indiana; the former on more mesophytic areas and the latter on more xerophytic areas, while *Tsuga* or *Tsuga-Pinus* associations occupy very few circumscribed areas intermediate in mesophytism between the other two segregates. None of the genera mentioned by Nichols as occurring with *Tsuga* and *Pinus* in the area under consideration in his paper is found with them in Indiana except *Fagus*, *Acer* and, less commonly, *Quercus* and *Carya*.

In Table I is given the average percentage of available soil moisture (total moisture minus wilting coefficient) for weekly periods from May to September in *Tsuga*, *Tsuga-Pinus* and *Fagus-Acer* areas. It will be

TABLE I

AVERAGE AVAILABLE MOISTURE IN TSUGA OR TSUGA-PINUS AND FAGUS-ACER ASSOCIATIONS, MAY TO OCTOBER

	SOILS			
PINE HILLS, 1931	Surface	3-Inch	6-Inch	12-Inch
Mature Fagus-Acer	13.18		7.85	7.72
Mature Tsuga-Pinus on Slope.....	10.98		3.48	3.88
Mature Tsuga-Pinus on Terrace.....	10.68		6.64	4.56
TREVLAAC, 1930 (4, 5)				
Mature Fagus-Acer	12.27	4.89	3.89	
Mature Tsuga	7.67	2.89	2.55	
Seedling Fagus-Acer	9.84	1.78	2.36	
Seedling Tsuga	7.26	1.78	2.67	
TURKEY RUN, 1929 (3)				
Mature Fagus-Acer	18.6	15.2	9.3	9.8
Mature Tsuga	7.7	-0.7	-1.3	-2.1

TABLE II

TIME IN WEEKS DURING WHICH SOIL MOISTURE IS BELOW WILTING COEFFICIENT IN FAGUS-ACER AND TSUGA OR TSUGA-PINUS ASSOCIATIONS

		SOILS			
PINE HILLS, 1931		Surface	3-Inch	6-Inch	12-Inch
Mature Fagus-Acer	6			6	0
Mature Tsuga-Pinus (Slope)	6			8	8
Mature Tsuga-Pinus (Terrace)	0			0	1
TREVLAAC, 1930 (4, 5)					
Mature Fagus-Acer	5	7		9	
Mature Tsuga	9	9		12	
Seedling Fagus-Acer	5	10		9	
Seedling Tsuga	10	11		11	
TURKEY RUN, 1929 (3)					
Mature Fagus-Acer	0	0		0	0
Mature Tsuga	5	6		6	12

seen that in almost every case, whether it be in mature stands or in seedling stands, the average percentage of available moisture in Tsuga or Tsuga-Pinus areas is less than in Fagus-Acer areas, and in most cases the differences are considerable.

Not only is the average summer soil moisture less in Tsuga and Tsuga-Pinus areas than in Fagus-Acer areas, but in all cases except the

Tsuga-Pinus association occurring on a second terrace area in the Pine Hills district, the number of weeks during which the soil moisture content went below the wilting coefficient is greater in Tsuga and Tsuga-Pinus areas than in Fagus-Acer areas. Even in case of the Tsuga-Pinus second-terrace area, where the moisture content did not go below the wilting coefficient (Table II) so often as in the Fagus-Acer area, the content was near the wilting coefficient more often than in Fagus-Acer, so that the average available moisture is higher in the latter.

Clements (2) has shown that a relict association inhabiting a situation which is somewhat more xerophytic and located within what is generally a more mesophytic area should be considered a preclimax association, while one which occupies a somewhat more mesophytic situation located within what is generally a more xerophytic area should be considered a postclimax relict association. If these soil-moisture relations are definitive of the type of forest-climax relict, then Tsuga and Tsuga-Pinus associations in Indiana must be considered to be preclimax relicts, since they inhabit here more xerophytic situations as vegetative islands surrounded by more mesophytic Fagus-Acer areas.

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